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NAME OF AUTHOR/*NOM DE L'AUTEUR* Brett K. Calverley

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NAME OF SUPERVISOR/*NOM DU DIRECTEUR DE THÈSE* D. A. Boag

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PERMANENT ADDRESS/*RÉSIDENCE FIXE* 115-48-80 Ave.
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THE UNIVERSITY OF ALBERTA

A COMPARATIVE STUDY OF REPRODUCTIVE POTENTIAL IN PARKLAND- AND ARCTIC-NESTING MALLARDS AND PINTAILS (ANATIDAE)

by

© BRETT K. CALVERLEY

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

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EDMONTON, ALBERTA

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FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled "A comparative study of reproductive potential in parkland- and arctic-nesting mallards and pintails (Anatidae)" submitted by Brett K. Calverley, in partial fulfilment of the requirements for the degree of Master of Science.

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Supervisor

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Date ..June 19, 1975

ABSTRACT

In this study, I collected samples of female mallards and pintails from populations in the Alberta parklands near Tofield, and in the Mackenzie River Delta, Northwest Territories, in order to determine the proportions that were reproductively active, to estimate the potential clutch size of each species in each area, to determine the age structure of the two populations in each area, and to calculate the energy drain associated with migration and reproduction of females homing to the Mackenzie Delta and those displaced there from the parklands.

Eighty mallards and 94 pintails were collected shortly before, during, or shortly after the laying period. Reproductive potential was determined, based on the condition of the ovaries and oviducts of collected ducks; it was found to be significantly lower in the Mackenzie Delta than in the Tofield area for both species. This was because the proportion of reproductively active mallards and pintails was significantly lower ($P < 0.005$) in the north than in the south, the average clutch size was significantly lower ($P < 0.005$) in the north than in the south and renesting was not recorded in the north but was in the south. The technique used to determine the absolute age of collected birds failed to produce satisfactory results. Therefore, the low reproductive potential in the north could not be attributed to any particular age class. Estimates of energy costs suggested that of those females displaced because of drought on the prairies only those with significantly greater than the average amounts of stored fat would have had sufficient energy to enable them to lay eggs in the north. Further, the energy drain caused by delayed laying in 1974 was sufficient to

reduce average potential clutch size in the north and to reduce the proportion of female mallards and pintails, which were reproductively active.

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INTRODUCTION

Each spring vast numbers of waterfowl migrate north to breed where appropriate habitat is available in Alberta and the District of Mackenzie. Farner (1973:1) states: "The phenomena of discontinuity and periodicity in reproduction have been enhanced, in evolution, by the selection of control systems that cause reproduction to occur when environmental conditions maximize the probability of survival of the young, and minimize hazards to the reproductive adults." Presumably this migratory pattern has evolved to meet these conditions.

Female mallards (*Anas platyrhynchos*) and pintails (*A. acuta*) usually nest where sufficient resources are available to fill the requirements of both the parents and the young (Farner 1973). The availability of these resources, particularly surface water, varies considerably from year to year on the prairie portions of the breeding habitat. The effect of these fluctuations on the distribution and reproductive success of these ducks remains largely a subject for speculation (Crissey 1961; Hansen and McKnight 1964; Smith 1970; Henny 1973).

Henny (1973) discusses banding returns among pintails. Implicit in his discussion are two groups, one breeding in the prairie-parkland region and another in the arctic. Thus it is likely that among both mallards and pintails there are those that normally nest in the prairie-parkland region and those that normally nest in subarctic and arctic. There is probably some degree of interchange between these groups (Henny 1973), the extent of which is partially dependent upon availability of resources in the prairie-parkland region (Hansen and McKnight 1964).

The key resource in the parklands is surface water (Lynch *et al.* 1963). This in turn is dependent upon annual precipitation and the degree to which melt-water in spring is lost as runoff. Data based on aerial counts of waterfowl (Anonymous 1955-1974) suggest that during periods of drought (1958-1962), when the area of surface water was significantly reduced, the total population of North American ducks also declined significantly (Crissey 1961).

The prairies contain approximately ten million natural depressions, and although they are never all filled at the same time (Gollop 1965 in Cooch 1969) they represent the habitat type which has the greatest density of breeding mallards and pintails (Anonymous 1955-1974). These water-filled depressions or ponds are hereafter referred to as potholes. Waterfowl have evolved particular behavioral patterns that permit them to apportion the available breeding habitat (McKinney 1965). This author found that as these ducks return to this area each spring, they disperse from flocks and attempt to establish home ranges near the site where the female of the pair was raised. In this way the available habitat is filled. If potholes are scarce, as in drought years, mallards are reported to be able to condense their home ranges somewhat, and thus increase their density (Anderson and Henny 1972); no such ability has been reported for pintails. Thus, when sufficient habitat is not available for all individuals, some are unsuccessful in establishing home ranges (Rogers 1964; Smith 1969) and must move elsewhere.

Aerial census data (Anonymous 1955-1974) suggest that unsuccessful pairs may continue in a northward direction until suitable unoccupied habitat is encountered. Subarctic and arctic breeding grounds are the last areas into which such displaced breeding pairs can move. Thus, when

drought occurs, some females of both species, that would have normally nested on the plains, apparently join those that normally nest in the arctic (Hansen and McKnight 1964). It has been suggested that a relatively stable number of birds nest annually in the north despite occasionally very abundant wetland habitat in the south over which they may or may not migrate (Hansen and McKnight 1964; Henny 1973).

From the standpoint of North American populations of these two species, it is important to know the impact of this reported displacement on their reproductive potential. Is it different from populations that were able to become established in the south? Is it different from that population reported to breed annually in the north? Hansen and McKnight (1964) reported that only some supposedly drought-displaced females of several species did produce broods apparently of normal size in Alaska.

Sowls (1955) provided evidence that older, more experienced, female pintails arrived first on the breeding grounds; the same was true for female gadwalls (*Anas strepera*) (Gates 1962). Thus, it may be primarily yearling ducks that are drought-displaced (McKinney 1965). Female ducks nesting for the first time tend to lay smaller clutches (Grice and Rogers 1965; Dane 1966; Mihelsons *et al.* 1968). Thus one might expect smaller average clutch size in the north in drought years on the prairies. Reproductive potential is reduced only if displaced females did not nest, laid fewer eggs than they would have in the south, and/or were unable to renest when losing their first clutch. Smith (1970) provides evidence to indicate that a reduced reproductive potential may in fact be the case, based on declining proportions of juveniles in the hunter kill.

The hypothesis then becomes: when periods of drought occur on the prairies many yearling female mallards and pintails are displaced northward and in so doing their reproductive potential is greatly decreased.

The objectives of this study were: (1) to determine the proportions of reproductively active female mallards and pintails in samples collected from populations in the parklands of Alberta and in the Mackenzie River Delta, N.W.T.; (2) to determine the potential clutch size of each species in each area; (3) to determine the age structure of the two populations; and (4) to calculate the energy requirements of females homing to the western Canadian arctic and those females being displaced there from the parklands of Alberta.

STUDY AREAS

1. Southern

Female mallards and pintails were collected in an area 64 kilometers east of Edmonton, south of Highway 14, and bounded by Lindbrook (Beaver) County Hall and the towns of Ryley, Round Hill and Kingman. I refer to this as the Tofield study area (Fig. 1). This study area encompassed approximately 518 square kilometers and was situated in the parkland ecotone of central Alberta (Moss 1932; Bird 1961). The western edge of the study area abuts on the Cooking Lake moraine, which is of knob-and-kettle topography and predominantly forested with aspen (*Populus tremuloides*). To the east this area quickly merges into relatively flat, predominantly agricultural land given over to cereal crops. Within this area were occasional woodlots of aspen and small meandering creeks with which cattle were often associated.

The area was excellent breeding habitat with an interspersion of potholes including some very large ponds and one lake just north of the study area. Most ponds typical of the glaciated prairies were well represented (Stewart and Kantrud 1971). Breeding pairs of mallards and pintails appeared to be nearly equally represented on the study area.

The spring of 1973 was very dry both on the prairies to the south and in this parkland area. Ephemeral melt-water ponds, so important to mallards and pintails, were few in number in this year (Table 8). By contrast, the spring of 1974 was one of abundant water throughout the prairie-parkland region (Table 8). Thus the conditions for waterfowl in the two springs were very different and could be expected to support

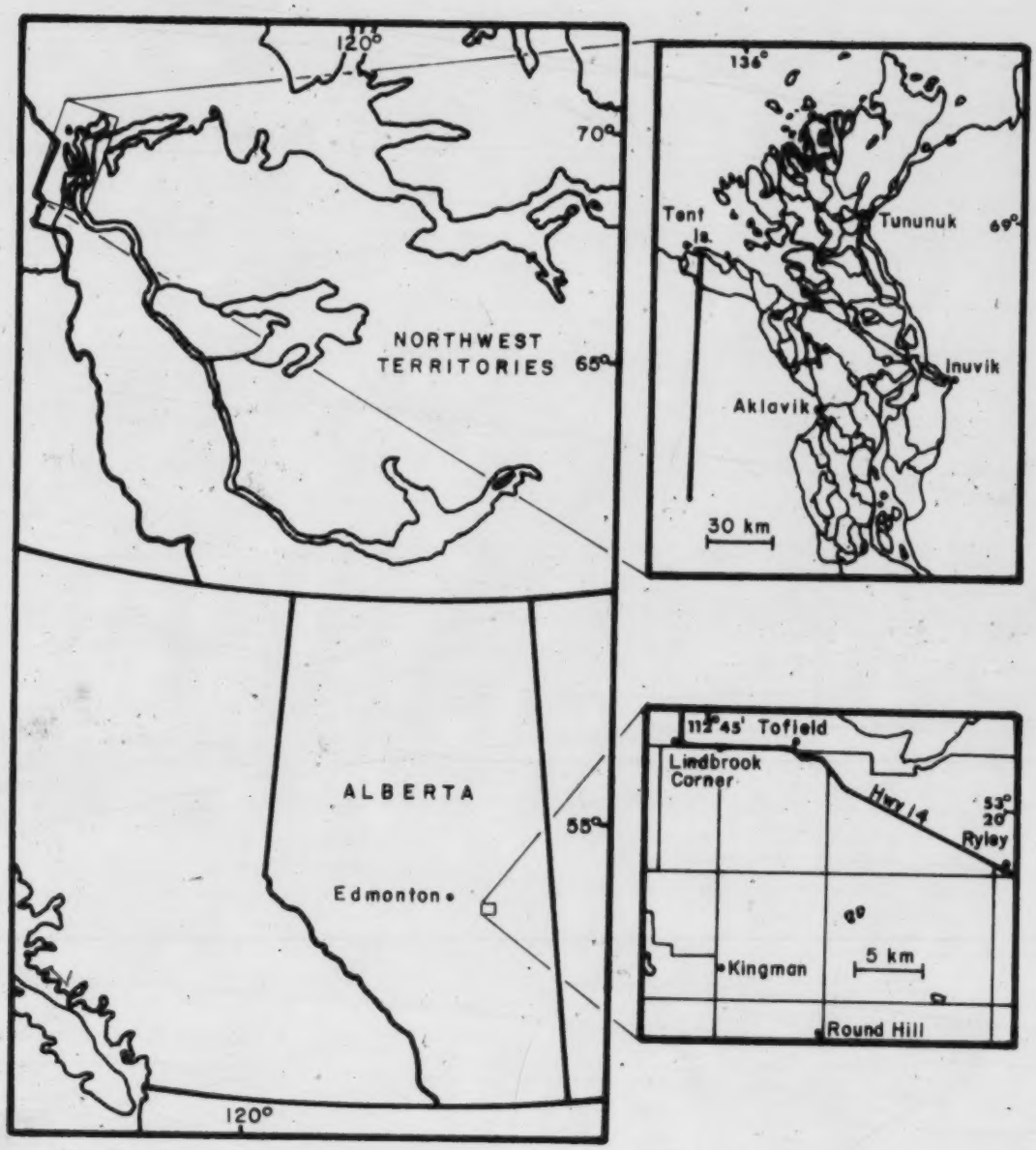

FIGURE 1. The locations from which populations of mallards and pintails were sampled during the breeding seasons of 1973 and 1974: the Tofield area in Alberta and the Mackenzie Delta area in the Northwest Territories.

relatively much larger numbers of nesting ducks in the latter year.

2. Northern

The 13,000 km^2 (5,000 square-mile) Mackenzie River Delta (Smith *et al.* 1964) is a major arctic waterfowl breeding area (Porsild 1935; Cowan 1948; Banko and Mackay 1964; Barry 1964; Smith *et al.* 1964; Wellein and Lumsden 1964) and was the area from which mallards and pintails were sampled in the north (Fig. 1). The Delta has a treeless zone in the north and a forested zone in the south (Lambert 1972). Porsild (1935) and aerial census data (Anonymous 1955-1974) indicate that equal but only moderately sized populations of mallards and pintails exist in the forested area, and that large pintail and small mallard populations are present in the northern treeless area. I therefore chose to collect in the transition zone (Lambert 1972) where I hoped to find reasonable numbers of both species. However, such was not the case, as mallards were scarce, being far less numerous than pintails. This necessitated movements over somewhat larger areas.

The area most intensively sampled was the central triangle of the Delta, bounded by Inuvik, Aklavik and Tununuk Point. In 1974, however, the whole northern half of the Delta from Inuvik and Aklavik to Tent Island and Tununuk (approximately 6,500 km^2) was searched; birds were sampled where encountered.

The Mackenzie River Delta represents a strange breeding ground for these so-called "prairie ducks" (Sowls 1955). These birds are subjected to such stressful climatic factors as low temperature and precipitation as both rain and snow, as well as physical factors such as push ice and flooding at the time of spring breakup. All these factors

have an important effect on the reproductive potential of mallards and pintails in this location.

METHODS AND MATERIALS

This study was based upon birds collected during the laying period. Occasionally females were collected just prior to the initiation or shortly after completion of their clutches. On the Tofield study area I shot samples of female mallards and pintails between April 23 and May 23 in 1973 and April 23 and May 7, 1974. At this time of year both species, but especially pintails, used shallow, melt-water ponds in harvested, fallow, and planted fields, or in pastures where surrounding cover was often completely lacking. Such situations offered little concealment, making approach within shooting range difficult. For this reason pintails were more difficult to collect than mallards, although relative densities were judged similar.

I collected samples in the Mackenzie Delta between June 3 and June 27 in 1973, and between May 24 and June 28, 1974. Because the onset of the reproductive cycle of these species is approximately one month later in the Mackenzie Delta than at Tofield, I was able to sample both populations at about the same stage of the cycle.

In the Tofield area I was able to drive along country roads and collect ducks in nearby ponds. Such was not possible in the Mackenzie Delta where a boat was necessary once open water was present. Before there was open water I used a sled and snowmobile. The snowmobile was used to drag the boat which was placed on the sled for long-distance travels. By quickly moving along the open leads of the major water courses before break-up and along the creeks, rivers, channels and lakes after break-up, I was able to surprise ducks and shoot them from the boat.

Of the two species, pintails again were found to be the most difficult to approach. Not only did they frequent the exposed shorelines of the main channels, but they were also more flighty, often flushing well ahead of the boat. Nevertheless, shooting from the boat proved the most successful method for collecting. Mallards tended to be less flighty but in many cases also flushed well ahead of the boat.

I recorded the following information from each female shot: date, time of day, location, weight, and social status (unpaired, paired or flocked). I then removed the ovary and oviduct, and put them in unsealed plastic bags to cool, in ice or snow when available. These organs were then fixed in 10 percent formalin as soon as possible. The rest of the carcass was preserved by freezing.

Examination of the reproductive organs enabled me to place the ovaries and thus the ducks into the following categories of reproductive status: pre-ovulatory, ovulatory, post-ovulatory, pre- and post-ovulatory, atretic, and non-ovulatory. The criteria used in deciding the category into which ovaries were placed were as follows: pre-ovulatory--ovary possessed pre-ovulatory follicles that were both pale yellow in color and were gradated in size, the largest being more than 20 mm, but lacked any post-ovulatory follicles; ovulatory--ovary possessed at least one pre-ovulatory follicle of sufficient size to ovulate within 24 hours and possessed at least one post-ovulatory follicle of a size that would indicate less than 24 hours from ovulation; post-ovulatory--ovary possessed no pre-ovulatory follicles (large enough to shed an ovum within 24 hours) but possessed a number of post-ovulatory follicles; pre- and post-ovulatory--ovary possessed many small post-ovulatory follicles and pre-ovulatory follicles gradated in size, the largest being more than

20 mm in size; atretic--ovary possessed many pre-ovulatory follicles of varying sizes that were soft, pale in color and mottled when unfixed (Barry 1962) and possessed white deposits on their surfaces when fixed in 10 percent formalin, but lacked post-ovulatory follicles; non-ovulatory--ovary possessed only small pre-ovulatory follicles gradated in size, none more than 14 mm in width, but lacked post-ovulatory follicles.

From observations on color and measurements of width and volume of all pre-ovulatory, post-ovulatory and atretic follicles, the number of eggs a duck was going to lay (potential clutch size) was estimated. Only those pre-ovulatory and atretic follicles greater than 3 mm in width were measured. Diameter was measured along the stigma in pre-ovulatory and atretic follicles and along the line of rupture in post-ovulatory follicles using dial calipers, and volume, by water displacement. The volume of the oviduct also was measured using water displacement. This latter measurement was a useful check, when compared to the state of the ovary, in the determination of reproductive status.

The technique used in an attempt to determine the absolute age of the birds collected is given in Appendix 1.

Differences in sets of data were tested statistically by Chi-square (when comparing proportions) and by the Wilcoxon's Two Sample Test (when comparing medians). Analysis of linear regression was used to test the significance of correlation coefficients. Differences were considered significant if the probability level was less than 5 percent.

RESULTS

Number of Specimens Collected

During the two seasons of this study, I was able to collect a significantly larger ($P < 0.01$) sample of female mallards and pintails in the Tofield area than in the Mackenzie Delta (127 vs. 47; Table 1). There were no significant differences between species in the number taken in any one year; nevertheless the total numbers of pintails taken in the Mackenzie Delta did significantly exceed that of mallards (33 vs. 14; $P < 0.01$).

Analysis of Reproductive Status

The first parameter of reproductive potential measured in this study was reproductive status, that is, whether a female was, or was not, reproductively active. Reproductive status of female mallards and pintails collected during the nesting period was based on the condition of the reproductive organs (ovary and oviduct) or on evidence of incubation (brood patch as described by Welty 1962:301).

The condition of the reproductive organs and hence the stage in the reproductive cycle at which ducks were shot is presented in Table 2. Ducks falling into the first four categories (pre-ovulatory, ovulatory, post-ovulatory and pre- and post-ovulatory) were reproductively active and into the last two (atretic and non-ovulatory), not reproductively active. The table does not include two pintails collected at Tofield on April 17, 1974, too early to decide whether or not the ovarian follicles would develop. However, it does include one mallard collected at Tofield

Table 1. Numbers of female mallards and pintails collected at Tofield and the Mackenzie Delta, 1973-74

Species	Year	Study Area	
		Tofield	Mackenzie Delta
Mallards	1973	35	8
	1974	31	6
Pintails	1973	29	20
	1974	32	13

Table 2. The reproductive status of mallards and pintails collected from the Tofield and Mackenzie Delta areas (1973-1974)

Species	Location	Year	Categories of reproductive status						Total
			Pre-ovulatory	Ovulatory	Post-ovulatory	Pre- and Post-ovulatory	Atretic	Non-ovulatory	
Mallards	Tofield	1973	5	20	2	5	1	2	35
		1974	8	21	1	0	0	1	31
	Mackenzie Delta	1973	0	4	2	0	1	1	8
		1974	0	2	2	0	2	0	6
Pintails	Tofield	1973	6	19	2	1	0	1	29
		1974	5	22	2	1	0	0	30
	Mackenzie Delta	1973	1	10	0	0	2	7	20
		1974	0	5	4	0	2	2	13
Total (% of grand total)			25 (15%)	103 (60%)	15 (9%)	7 (4%)	8 (5%)	14 (8%)	172

in 1974, that was physically incapable of laying an egg because massive adhesions of the gut and oviduct at the cloaca would have prevented passage of an egg.

Female mallards and pintails in all categories of reproductive status were represented among the samples shot (Table 2). Of 172 birds, 25 (15 percent) were categorized in the pre-ovulatory group. The number of ducks in this class among the Tofield specimens was significantly greater ($P < 0.01$) than among those from the Mackenzie Delta. Nevertheless, this difference cannot be attributed to an earlier sampling period, relative to the reproductive cycle, at Tofield, because the distribution of dates on which these ducks were shot did not vary significantly from randomness. Most ducks shot (103) fell into the ovulatory category. The proportion of ovulatory females collected at Tofield was significantly greater ($P < 0.05$) than that collected in the Mackenzie Delta. Only 9 percent of the females collected were in the post-ovulatory category. Fifty percent of these were shot late in the collection periods with the remaining 50 percent distributed throughout the early to middle phases of collection. All were birds collected while off the nest or that had recently lost their clutch of eggs. Thus, collection periods seem to have been optimal with most in the ovulatory stage and relatively fewer birds in the pre- and post-ovulatory stages. The renesting category (pre- and post-ovulatory category) had the lowest proportion (4 percent) of shot females. The proportion of females renesting in 1973 (6/64) at Tofield was not significantly greater than in 1974 (1/61). It is noteworthy that none of the Mackenzie Delta samples contained any renesting individuals. Females with ovarian follicles undergoing atresia made up 5 percent of all females collected

and were shot during only the first half of the collection periods. There was a significantly greater ($P < 0.01$) proportion of females in this category from the Mackenzie Delta (7/47) than from Tofield (1/125). Likewise, there was a significantly greater ($P < 0.01$) proportion of females in the non-ovulatory category from the Mackenzie Delta (10/47) than from Tofield (3/125). This difference was due mainly to the Mackenzie Delta pintail contribution to this category in 1973.

Summing up, of 125 female mallards and pintails sampled from the parkland habitat, 120 (96 percent) were reproductively active when shot, whereas of 47 specimens of these species shot in the Mackenzie Delta, only 31 (64 percent) fell into this category (Table 2). Thus, significantly more mallards ($P < 0.05$) and pintails ($P < 0.01$) were reproductively active on the Tofield study area than on the Mackenzie Delta area over the period of the study (Table 3). There was no significant difference between years, or species, within the same location.

Date of Clutch Initiation

The length of time available for ducks to begin laying will influence the reproductive potential of ducks through their ability to renest. Thus I determined the date of clutch initiation for ducks that were soon to commence laying, that were laying, and that had completed laying. In those birds which had not yet begun to lay I estimated the date of laying by comparing the size of the largest pre-ovulatory follicle to a growth curve for such follicles (Fig. 2). In birds that were still laying I was able to determine the date of laying the first egg of the clutch, by counting the number of post-ovulatory follicles and

Table 3. The proportions of female mallards and pintails, judged to be reproductively active, among samples taken from the Tofield and Mackenzie Delta areas (1973-74)

Species	Year	Location			
		Tofield		Mackenzie Delta	
		Proportion	%	Proportion	%
Mallards	1973	32/35	91	6/ 8	75
	1974	30/31	97	4/ 6	67
Pintails	1973	28/29	97	11/20	55
	1974	30/30	100	9/13	69

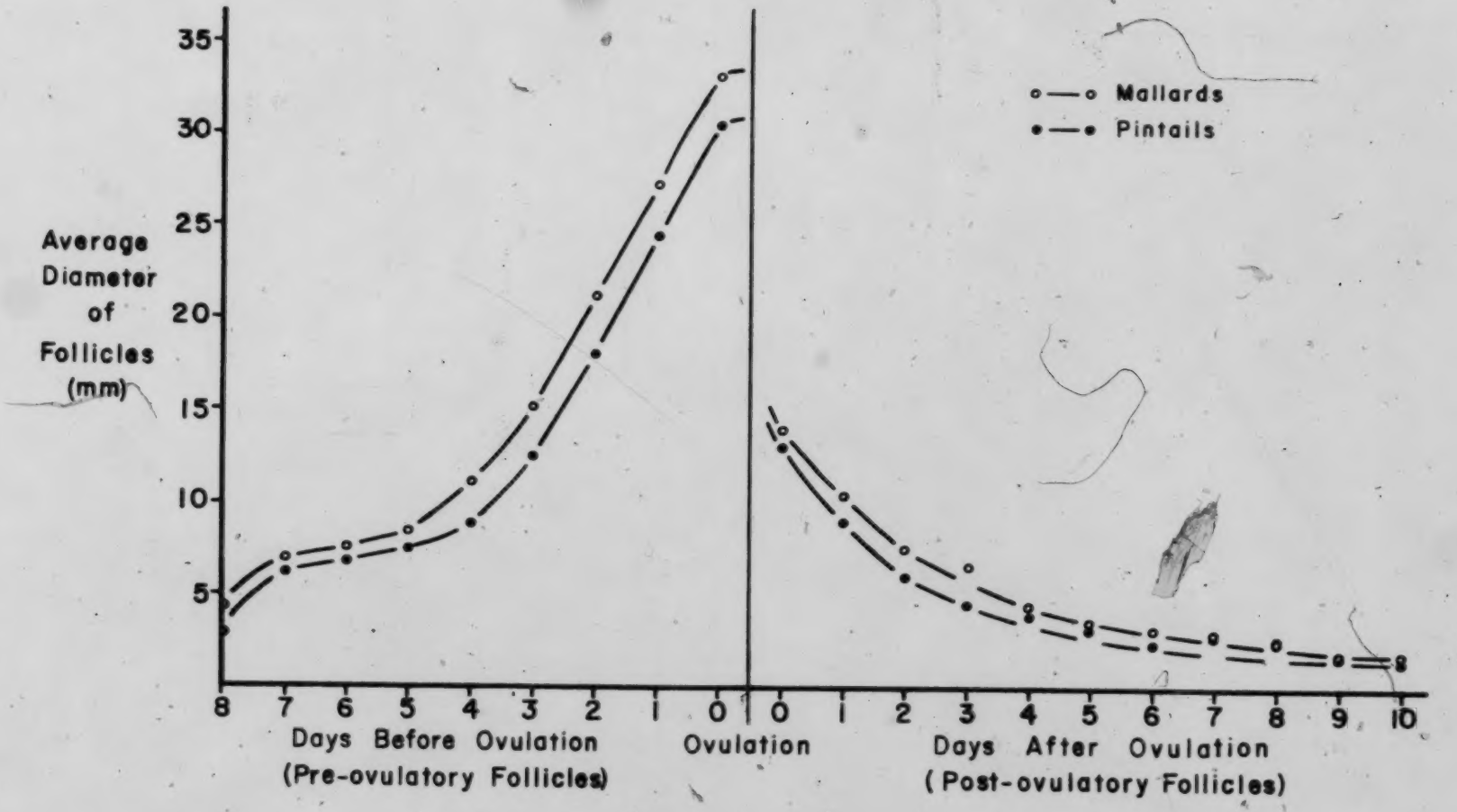

FIGURE 2. Growth of pre-ovulatory and regression of post-ovulatory follicles in mallards and pintails. Curves fitted by eye.

back-dating 1 day for every egg laid (Sowls 1955). For those birds that had completed their clutches, I counted the number of post-ovulatory follicles and noted the size of the largest post-ovulatory follicle. By comparing the latter to a regression curve of post-ovulatory follicles (Fig. 2) I was able to estimate the date of laying the last egg to which were added the number of days equal to the number of post-ovulatory follicles.

Mallards and pintails in the Tofield samples began laying significantly earlier ($P < 0.001$) than those from the Mackenzie Delta (Fig. 3). At Tofield, the laying periods for mallards and pintails were different in the 2 years of the study. In 1974, the laying period was significantly earlier ($P < 0.01$) than in 1973, and laying was also concentrated over a shorter period of time in 1974, than in 1973 (among mallards - 21 days vs. 35 days; among pintails - 14 days vs. 24 days). The distributions of dates of clutch initiation for the Mackenzie Delta samples do not show the same significant separation in the 2 years that was evident at Tofield. Nevertheless, there is a suggestion (Fig. 2) that some birds, particularly mallards, were destined to nest earlier in the Delta in 1974, than in 1973. There was no significant difference in the onset of laying, between species, within the same year. However, Mackenzie Delta mallards, sampled in 1974, nested significantly earlier ($P < 0.025$) than pintails in the 1973 Mackenzie Delta sample.

Potential Clutch Size

Potential clutch size was estimated as another parameter of reproductive potential and was based on the size, color and number of pre-ovulatory and post-ovulatory follicles, and occasionally the presence

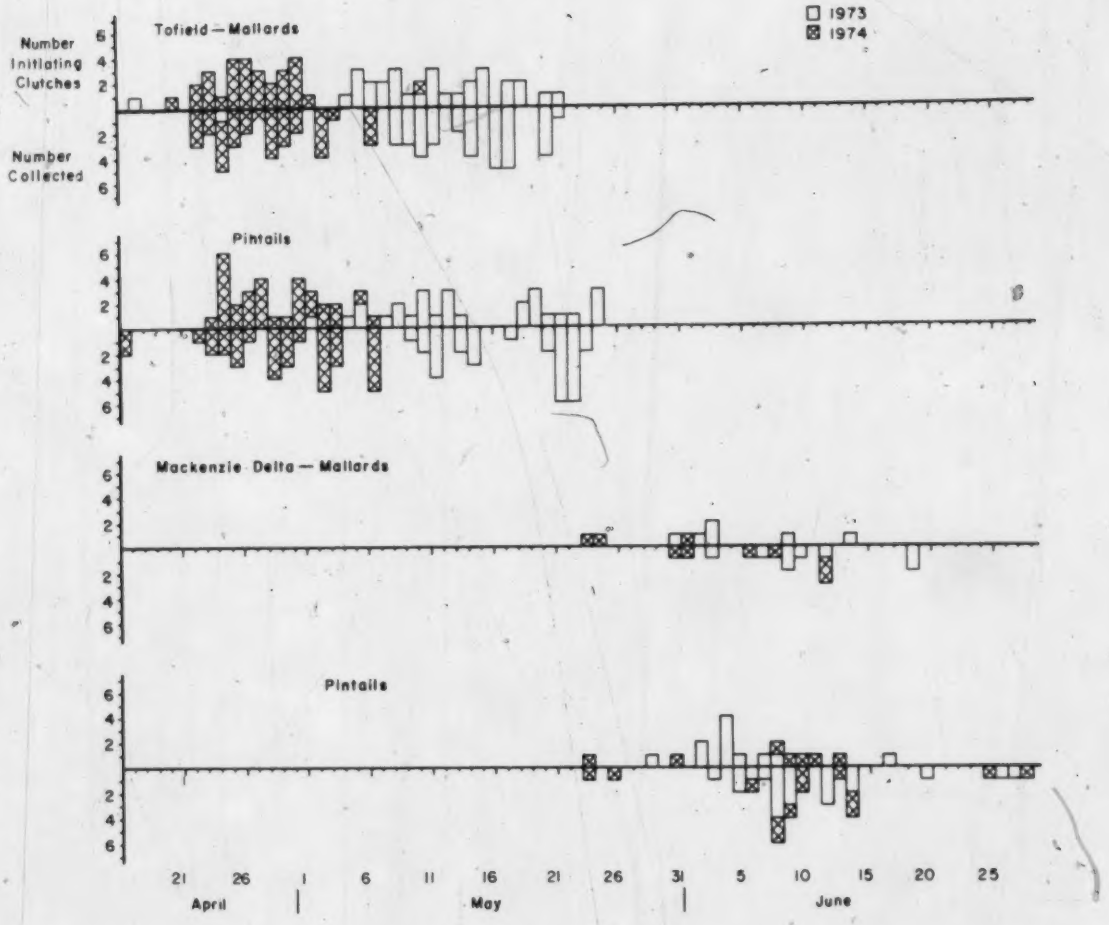

FIGURE 3. Frequency distribution of dates of onset of laying and collection among female mallards and pintails sampled from Tofield and the Mackenzie Delta (1973-74).

of atretic follicles. There were three basic problems in determining potential clutch size: 1) distinguishing small pre-ovulatory follicles that were destined to be shed from those that were not; 2) distinguishing somewhat larger pre-ovulatory follicles from those undergoing atresia; and 3) distinguishing small post-ovulatory follicles from small atretic follicles.

Growth of pre-ovulatory follicles is relatively slow until a width of approximately 7-8 mm is reached (Fig. 2). This corresponds with the stage of reproductive cycle referred to as "searching" by Sowls (1955), that is, when the female seeks a nest site. From this point on (presumably once a nest site or territory has been found), follicle growth increases rapidly to maximum size in about 5 days. It is evident that for mallards and pintails follicular growth follows the same general pattern, although follicles of pintails are slightly smaller in size. The regression rate for post-ovulatory follicles is rapid in the first 3 days, gradually leveling off until day 9, after which regression continues very slowly. Again, the pattern for mallards and pintails is much the same.

Ovaries of shot specimens were sometimes damaged. However, by using Figure 2 and the average diameter and volumes of pre-ovulatory follicles ranked by size (Table 4), I was able to estimate the size of damaged follicles. Both diameter and volume were used in ranking the pre-ovulatory follicles (Table 4) because their shape sometimes deviated from a sphere, in which case it was difficult to get comparable diameters. Although measurement of diameter was easier to take than volume, the latter was a more accurate measure of size.

Table 4. Average diameters (mm) and volumes (ml) of developing pre-ovulatory follicles, ranked from largest to smallest. Standard deviations (SD) and sample sizes are included.

Species	Size characteristics	Rank of Pre-ovulatory follicles based on size								
		A	B	C	D	E	F	G	H	I
Mallards	Diameter	33.26	27.21	21.25	15.08	11.06	8.40	7.64	7.05	6.76
	SD	2.42	3.10	3.01	3.37	2.57	1.90	0.60	1.07	1.02
	Volume	14.43	8.58	3.88	1.59	0.63	0.27	0.20	0.16	0.14
	SD	2.48	2.22	1.37	1.09	0.37	0.10	0.05	0.05	0.05
	Sample size	39	40	39	45	41	25	18	12	8
Pintails	Diameter	30.39	24.44	17.89	12.40	8.72	7.31	6.70	6.20	5.62
	SD	2.30	2.63	3.21	2.66	1.89	0.88	0.85	0.73	0.62
	Volume	11.35	5.92	2.48	0.98	0.36	0.19	0.14	0.12	0.10
	SD	2.17	1.69	1.18	0.66	0.25	0.06	0.04	0.03	0.04
	Sample size	53	46	49	47	36	22	18	14	8

In Figure 4, a frequency distribution of size of pre-ovulatory follicles in the ovary of a laying pintail is graphed. In this case, all pre-ovulatory follicles less than 7 mm in width were judged to remain undeveloped, for two reasons: 1) if all of those follicles larger than 3 mm and smaller than 7 mm were destined to be shed, the potential clutch size would have been 26, a clutch size never recorded for pintails; 2) the large number of pre-ovulatory follicles in the lower size categories suggested that many follicles had grown to 5 mm, but only those destined to be shed were developing further. Thus the number of ovarian follicles judged to still be maturing in this case was five. For ducks shot well on in the laying cycle (Fig. 5), this problem was resolved because the gap appearing in the distribution of follicle sizes combined with the frequency of follicles in the smaller size categories, made it easy to distinguish the last ovum to mature. Thus, in Figure 5, only one ovum was still maturing. It was evident that the further along the duck was in the laying cycle, the easier it became to make this decision.

Having determined the number of pre-ovulatory follicles destined to be shed, I was able to add to it the number of post-ovulatory follicles present and thereby estimate the potential clutch size. Thus, for the bird represented in Figure 4 the number of pre-ovulatory follicles (five) plus the number of post-ovulatory follicles (six) gave this pintail an estimated potential clutch size of eleven. I used the presence of a gap in the frequency distribution of ranked pre-ovulatory follicles to estimate clutch size in 77 percent of all estimations of clutch size.

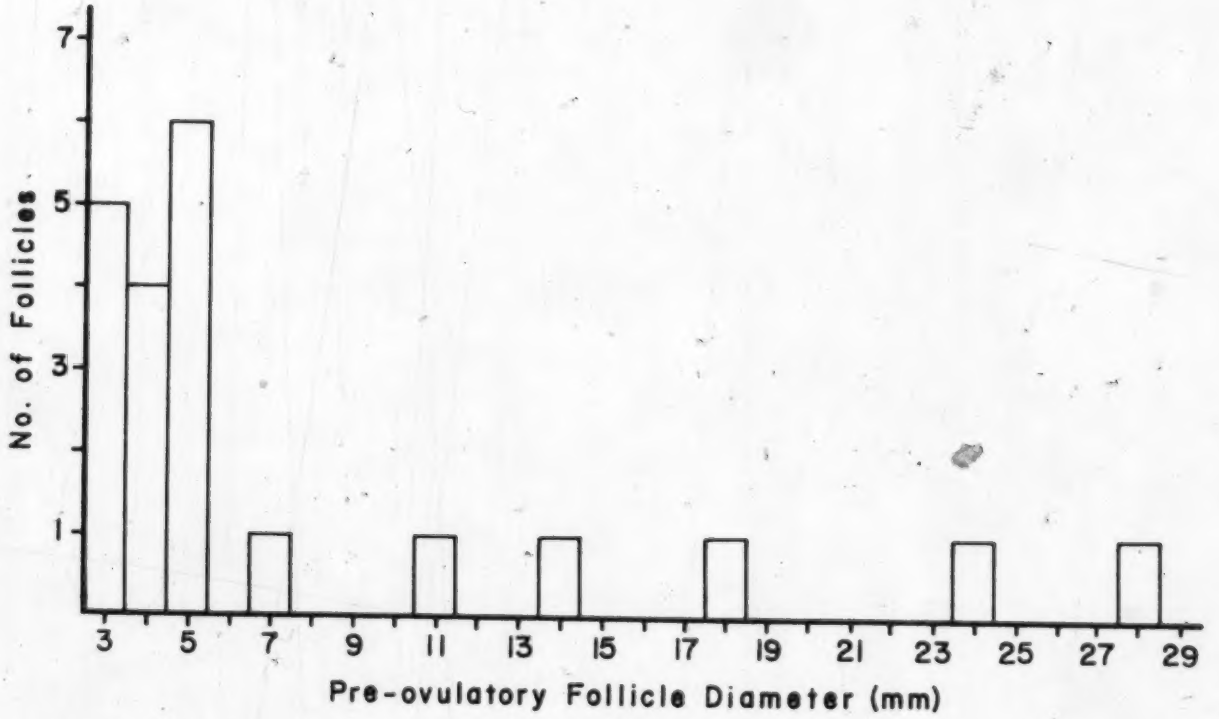

FIGURE 4. Frequency distribution of the size of pre-ovulatory follicles (greater than 2 mm diameter along the stigma) from the ovary of a pintail that had laid half its clutch.

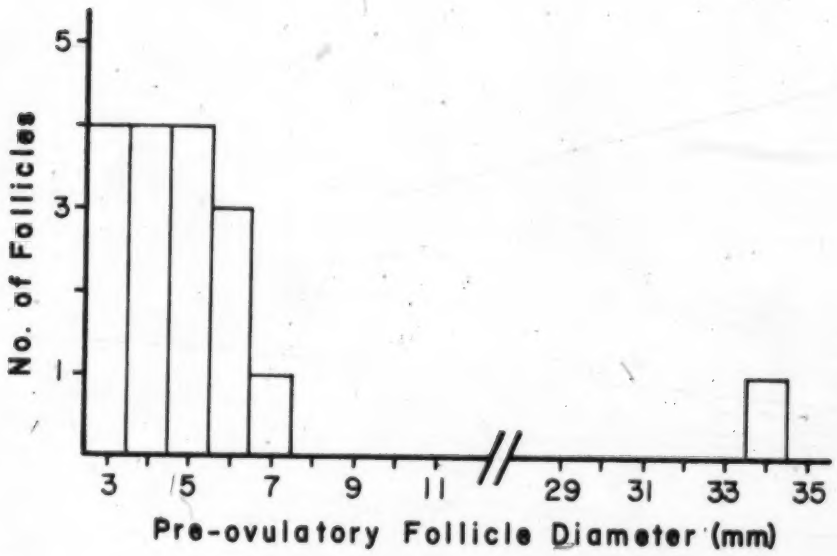

FIGURE 5. Frequency distribution of the size of pre-ovulatory follicles (greater than 2 mm diameter along the stigma) from the ovary of a pintail that had almost completed its clutch.

Figure 6 shows the frequency distribution of pre-ovulatory follicles for a pintail shot early in the reproductive cycle. For such a duck no gap in the frequency distribution was apparent. If all follicles exceeding 2 mm diameter from the ovary of this pintail (Fig. 6) were included, it would have had a potential clutch size of 19, again highly unlikely for this species. Therefore, in cases of this sort I resorted to the use of color in distinguishing maturing from non-maturing follicles. The follicles in the smallest size class that were yellow, rather than white, were estimated to be the last follicles destined to be shed. In Figure 6, follicles in the 4 mm size class were white, whereas those in the 5 mm size class were yellow. Thus, this pintail was estimated to have a potential clutch size of nine. I was forced to use this method of clutch determination in 19 of 150 (13 percent) cases. The basis for and reliability of the use of this color criterion are discussed later.

The problem of distinguishing small atretic follicles from post-ovulatory follicles has been encountered in other studies (Davis 1942; Lewin 1963; Payne 1966, 1973; Erpino 1969; Parmelee and Payne 1973). Most of the above authors sectioned follicles and examined them microscopically to make the distinction. Payne (1966) and Erpino (1969) found that in passerines post-ovulatory follicles were histologically distinguishable for only 10 to 12 days after incubation began. Lofts and Murton (1973) reported that, in the mallard, post-ovulatory follicles can be distinguished for 3 months.

To distinguish large pre-ovulatory follicles from those that had just begun resorption (atresia), I used the criteria described by Barry (1962:23). He referred to the atretic follicles of brant (*Branta*

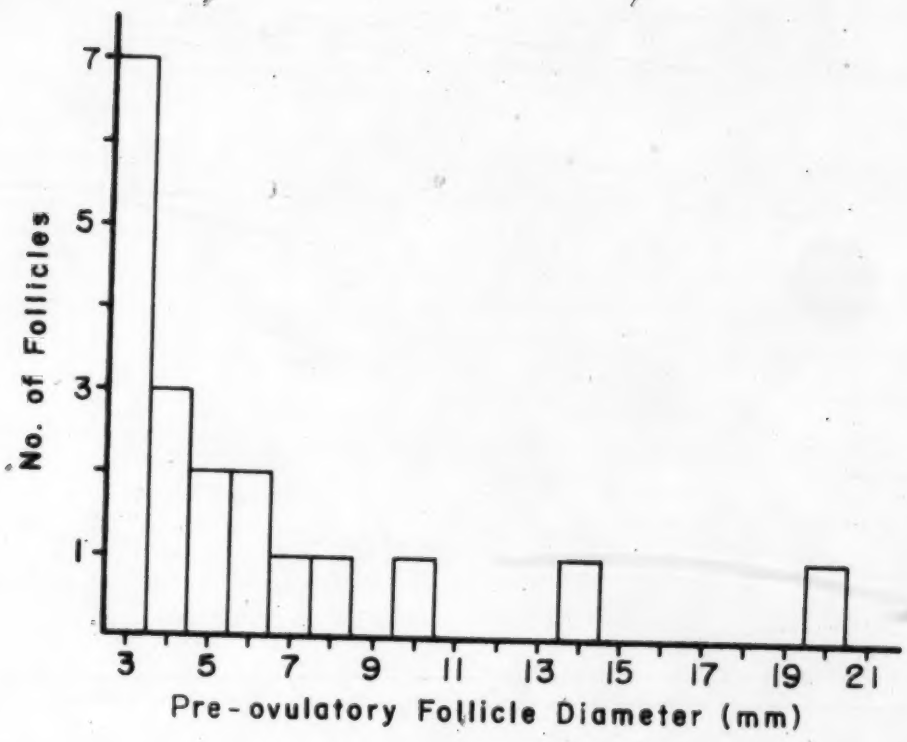

FIGURE 6. Frequency distribution of the size of pre-ovulatory follicles (greater than 2 mm in diameter along the stigma) from the ovary of a pre-laying pintail.

bernicla) and geese as being "flabby, like a deflated balloon." This description also applies to mallards and pintails when the follicles are fresh. However, when fixed in formalin they became firm and usually assumed a round shape when suspended in fluid. Therefore, the criterion for distinguishing these follicles in the fixed state was based on the presence of irregularities on the follicle surface, which were light colored against the dark yellow oocyte. These irregularities resemble fat deposits and, in fact, Lofts and Murton (1973) reported that the first histochemical indication of atresia was usually a lipoidal zone surrounding the oocyte which subsequently spreads throughout the interior of the follicle. Marshall and Coombs (1957) reported that this fatty atresia also was accompanied by invasion of the follicle by fibroblasts. Because atresia is essentially irreversible (Gilbert 1970), the presence of such a follicle in a gradient of developing follicles represents a gap in the developmental sequence (Gilbert and Wood-Gush 1971:1365). Thus, this "gap" can be considered analogously to an actual gap in the sequence and therefore represents the point beyond which no further follicles were destined to develop, enabling me to determine the potential clutch size in the three cases where this phenonemon was recorded.

For those ducks that had completed laying when shot, I could use only post-ovulatory follicles to estimate the number of eggs laid. In this study, ovaries of most females that fell into this category contained large, easily identifiable post-ovulatory follicles. However, in those cases when females had completed their clutches some days previously or were renesting, post-ovulatory follicles had regressed sufficiently to make the distinction between them and atretic follicles difficult. The stigma usually closes 9 days post-ovulation, and only then does the

identification of post-ovulatory follicles become difficult; only 2 percent of the post-ovulatory follicles examined had sealed stigmata. I distinguished regressed post-ovulatory follicles from atretic follicles by shape and by my ability to reopen the sealed stigma. Atretic follicles were more spherical than post-ovulatory follicles, which were quite flat. Payne (1966) found post-ovulatory follicles of blackbirds to be folded and wrinkled whereas atretic follicles were generally smooth. I observed no such difference in ducks. With the use of a dull probe the stigma of a post-ovulatory follicle, which had been closed only a few days was easily reopened.

Ducks collected at Tofield had a significantly larger ($P < 0.005$) potential clutch size than those from the Mackenzie Delta (Table 5). Thus the reproductive potential of the sampled mallards and pintails was lower in the north for the 2 years of this study. The potential clutch size for the combined 1974 samples was significantly lower ($P < 0.025$) than the combined 1973 samples. There were no significant differences, between years, for a given species in a particular location, except that Mackenzie Delta pintails collected in 1974 had a significantly lower ($P < 0.05$) potential clutch size than those in 1973. Likewise, the 1974 Mackenzie Delta pintails had a significantly lower ($P < 0.025$) potential clutch size than 1974 Tofield pintails and 1973 Tofield pintails. The potential clutch sizes of 1973 and 1974 Mackenzie Delta mallards, though lower in both years, were not significantly lower than Tofield mallards in the corresponding years. However, mallards from the Delta in 1974 did have a significantly lower ($P < 0.025$) potential clutch size than 1973 Tofield mallards. Thus, lower clutch sizes in the north were due to reduced potential clutch sizes primarily in 1974, when it was most pronounced in pintails.

Table 5. Estimated average potential clutch sizes of mallards and pintails sampled from the Tofield and Mackenzie Delta areas (1973-74). Numbers in parentheses indicate total number in samples which were reproductively active.

Species	Year	Tofield	Mackenzie Delta
Mallards	1973	9.7 (32)	8.2 (6)
	1974	9.0 (29)	7.5 (4)
Pintails	1973	8.8 (27)	8.5 (11)
	1974	8.5 (30)	6.4 (7)

It was not possible to compare the potential clutch sizes of initial and second clutches in the seven renesting females in this study. All but one of the renesting individuals had probably not completed their initial clutches, making it impossible to estimate the size of these first clutches. The individual for which the size of both clutches were estimated had a lower potential clutch size in its first attempt (7) than in its renest (10).

Energy Requirements for Reproduction in the Mackenzie Delta

In this section I examine the importance of energy (in the form of food and stored body fat) to the reproductive potential of laying female mallards and pintails. Further, I examine the impact of proximate factors such as temperature, precipitation, spring break-up and associated flooding on reproductive potential in a given year.

Figure 7 shows the average body weights of female mallards and pintails, collected at Tofield and in the Mackenzie Delta, at various stages of the reproductive cycle. The average weight of two female pintails collected on arrival at Tofield in 1974 was 25 percent more than the average weight of all other reproductively active female pintails taken at Tofield in 1974 (Table 6). I assumed this same differential existed for female mallards at Tofield although no specimens were taken on arrival. Assuming that these arrival weights are representative, both mallards and pintails showed a significant loss of weight in the immediate post-arrival period on the Tofield breeding grounds. This weight loss was assumed to have been associated primarily with energy consumption while establishing breeding space at a time when food energy available was probably insufficient to replace the energy expended.

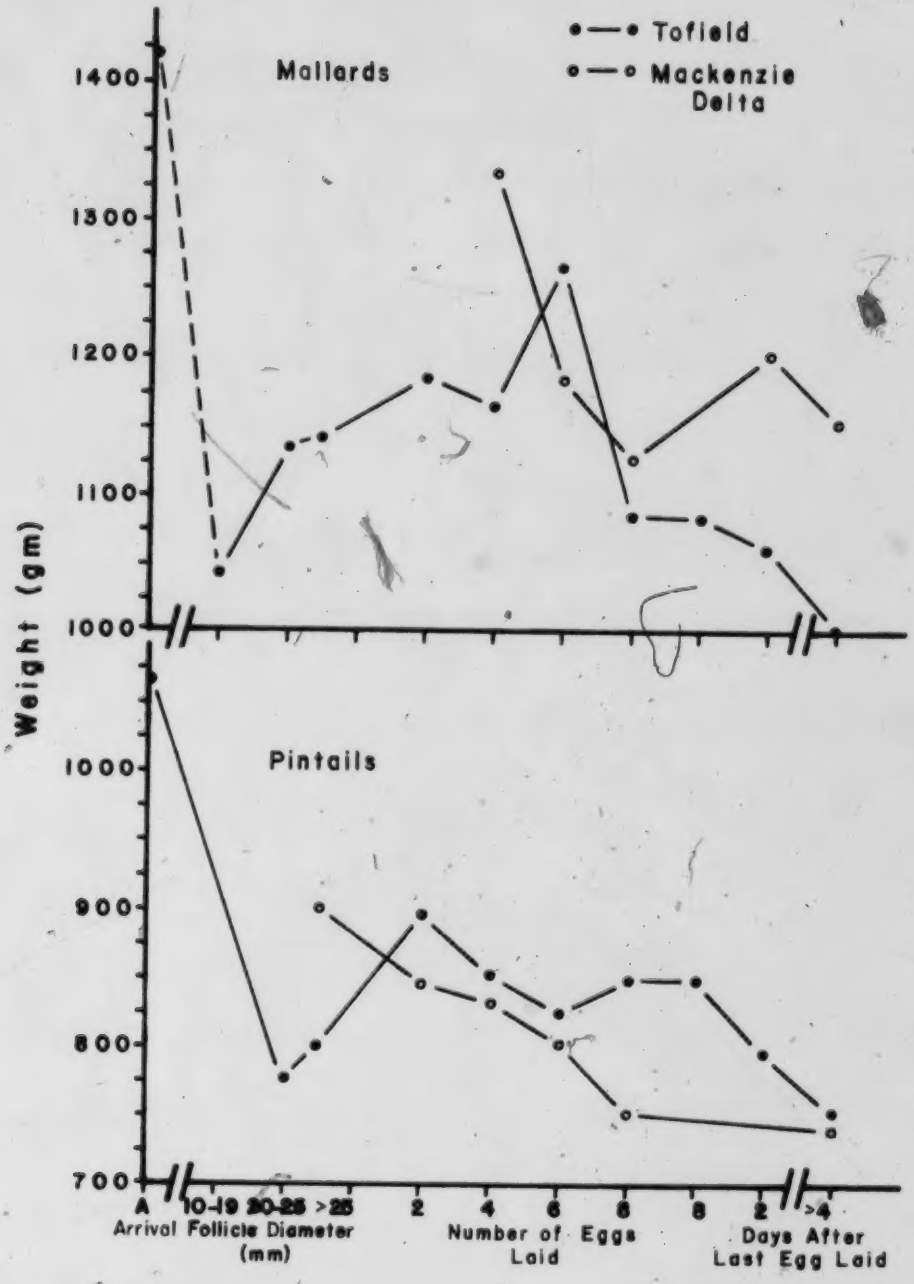

FIGURE 7. Relationship between weight of ducks and stage in the reproductive cycle. The interval shown approximates 2 days.

Table 6. Average weights, in grams, of reproductively active female mallards and pintails collected from the Tofield and Mackenzie Delta areas (1973-74). Numbers in parentheses indicate sample size.

Species	Year	Tofield	Mackenzie Delta
Mallards	1973	1121 (31)	1220 (5)
	1974	1190 (30)	1192 (3)
Pintails	1973	821 (28)	804 (10)
	1974	859 (30)	821 (9)

With the establishment of breeding space, the ovary and oviduct grew and the ducks regained lost weight by feeding on increasingly more available food of high protein and calcium content (Krapu 1974; Krapu and Swanson 1975), which they were able more effectively to exploit as the result of lower levels of intraspecific interactions resulting from the establishment of breeding space. Average body weight increased to a peak, at approximately mid-clutch in mallards, and the initiation of the clutch in pintails. This peak was 88 and 86 percent of arrival weight in mallards and pintails, respectively. Upon reaching this peak the average weights of these ducks declined probably as the result of laying and also because as the clutch neared completion more time was spent at the nest and less in feeding (Hochbaum 1944). Once incubation began weight declined quickly; females were feeding much less and the reproductive organs had regressed (Johnson 1961).

Average body weights of reproductively active female ducks in the Mackenzie Delta differed from those taken at Tofield (Fig. 7). Among pintails from the Mackenzie Delta, weight loss occurred at a relatively constant rate from pre-laying through to incubation (Fig. 7). Unfortunately no data were available on body weights in the Delta until 3-4 days prior to laying the first egg. Thus it is not possible to say whether these birds had regained weight after an initial heavy loss, such as the Tofield birds, or whether they had continued to lose weight slowly from the time of arrival. The amount of available food on arrival in the Delta was probably no more than on arrival at Tofield. Northern pintails weighed approximately the same, at the onset of laying, as did pintails in the Alberta parklands (Fig. 7).

In calculating energy requirements for reproduction in the Mackenzie Delta, for female mallards and pintails, I included energy costs of migration, body maintenance on arrival, and formation of eggs. Arrival weights for both species at Tofield were considered to be 25 percent greater than the average recorded body weights of reproductively active female mallards and pintails in the Tofield area (Table 6). Included in Table 6 are the average body weights of females collected from the Mackenzie Delta. There were no significant differences in weights between locations, or years, for either species except between the 1973 and 1974 mallard samples from Tofield ($P < 0.025$). This was due to the greater number of females, which had completed their clutches or were renesting when shot in 1973 over 1974 (7 vs. 1) and which consequently weighed less. When weights of birds in these categories were excluded, there was no significant difference. Thus the mean weight required for successful reproduction may be a species specific constant.

For females homing to the Mackenzie Delta, the net energy loss (grams of fat) between the time of arrival at the latitude of Tofield and departure for the north was considered negligible (Table 7) because such birds probably were not involved in establishing a home range at the latitude of Tofield and, if delayed en route, were probably able to consume sufficient food to maintain body weight while waiting to move on. However, those females of both species, that were homing to Tofield but were subsequently displaced northward, were estimated to have lost 9.4 percent of their body weight while attempting to establish breeding space, between the time of arrival at Tofield and departure for the Mackenzie Delta (Table 7). The 9.4 percent was used because it represented the percent reduction in weight between pre-laying (arrival)

Table 7. Energy requirements of migrating female mallards and pintails homing to the Mackenzie Delta or being displaced there from Tofield.

Description	Mallards			Pintails		
	Homing 1973	Displaced 1973	Homing 1974	Homing 1973	Displaced 1973	Homing 1974
Weight on arrival at Tofield (gm)	1400.6	1400.6	1487.3	1026.4	1026.4	1075.0
Maintenance cost while in the Tofield area (gm of fat)	--	131.7	--	--	96.5	--
Body weight on leaving Tofield (gm)	1400.6	1268.9	1487.3	1026.4	929.9	1075.0
Migration cost to the Mackenzie Delta (gm of fat)	88.4	82.3	92.3	70.6	65.7	73.0
Weight on arrival at the Mackenzie Delta (gm)	1312.2	1186.6	1395.0	955.8	864.2	1002.0
Maintenance cost while in the Mackenzie Delta before laying (gm of fat)	123.4	111.5	196.7	89.9	81.2	141.3
Hypothetical weight at laying (gm)	1188.9	1075.1	1198.3	866.0	783.0	860.7
Actual weight at laying (gm) of ducks that did lay	1348.2	1348.2	1285.8	872.4	872.4	881.0
Difference (gm)	-159.4	-273.1	-87.5	-6.4	-89.4	-20.3

and laying pintails in North Dakota (Krapu 1974). I am assuming that ducks actively attempt to establish breeding space and do not leave the southern breeding grounds until the energy normally associated with such behavior is expended without the acquisition of space.

The energy expended in migration from the latitude of Tofield to the Mackenzie Delta was calculated in the following manner: standard metabolism (basal metabolic rate) of female mallards and pintails was calculated using the equation -

$$M = 0.534\ W^{0.723}$$

where M = standard metabolism, and W = weight of bird in grams (Kendeigh 1970). LeFebvre (1964) states that the energy of flight is approximately 8 times the basal metabolic rate. Therefore using a distance of 1925 km (Hill 1972) and a flight speed of 80 km/hr (Sowls 1955), the energy equivalent required in terms of kilocalories, can be calculated for the flight from Tofield to the Mackenzie Delta. Odum *et al.* (1961) state that only reserve energy in the form of fat is used in migration. Using the caloric equivalent of one gram of fat (9.1 kcal: Johnston and McFarlane 1967; Johnston 1970), it was possible to estimate the reserve weight in grams of fat required for this migration (Table 7). Body maintenance costs between arrival and onset of laying in the Mackenzie Delta in 1973 was calculated using the same reduction factor (9.4 percent of arrival weight) as used previously (Table 7). However, for 1974, when spring break-up was about 10 days later (30 days after ducks arrived as compared to 20 days in 1973) and ambient temperatures were significantly lower ($P = 0.05$) females would have required more reserve energy for body maintenance until the time of laying. Assuming energy was expended at a

relatively constant rate during this period in both years, the energy expended in 1974 would have been 50 percent greater than that expended in 1973. Therefore, maintenance costs were based on a 14.1 percent reduction of body weight in 1974 (Table 7).

Using the above procedure, hypothetical average weights at onset of laying were determined for mallards and pintails. To compare these values with the actual average weight at the onset of laying of those ducks which did lay in the Delta, it was necessary to adjust the weights of these laying females when shot to their weights at the onset of laying. One indirect way to do this was to look at the relationship between body weight and time. If the relationship was significant, one could extrapolate to the weight at the onset of laying. There was a highly significant inverse relationship ($P \leq 0.01$) between body weight and the period of laying for pintails (Fig. 7). From the slope of this regression line I calculated the average daily weight loss during that period (15.4 gm). This weight loss represented 34 percent of the wet weight of a pintail egg. To calculate the average daily weight loss during the period of ovulation for a Mackenzie Delta mallard, 34 percent of the wet weight of a mallard egg was taken (20.1 gm). In this way the recorded weight of each laying Mackenzie Delta duck was adjusted to its weight at the onset of laying.

The dry weight of a mallard egg is 22.0 gm and of a pintail egg is 16.5 gm (egg weights based on data presented by Romanoff and Romanoff 1949). Thus in order that weight loss be balanced during the period of ovulation one must assume that at least 1.9 gm and 1.1 gm of dry weight came from the environment daily for mallards and pintails, respectively.

Even this is minimal because there must have been considerable environmental energy input to account for general body maintenance during this period.

Ducks have been observed feeding on plants such as *Equisetum fluviatile* and *E. arvense* in the Mackenzie Delta prior to break-up and these apparently retain a high protein content over winter (Don Gill pers. comm.). Thus perhaps much of the protein making up the eggs (Romanoff and Romanoff 1949) was ingested, however lipids incorporated into the egg probably were derived from stored body fat. Scott (1973) states that there is only sufficient calcium in the body of birds for two or three eggs. Therefore calcium must be ingested. Krapu and Swanson (1975) reported that most calcium required by laying pintails in North Dakota was ingested in the form of snail shells. Snail shells were observed to be abundant in the Mackenzie Delta, and were present in the esophagi of some of the pintails collected in the present study.

The differences between hypothetical weights at onset of laying and actual weights of laying birds adjusted to this time were calculated (Table 7). Negative values indicate that birds of average weight would not be able to lay a clutch of eggs equal in size to the recorded average clutch size for that year. Female mallards of average weight arriving at the latitude of Tofield (Table 7) and homing directly to the Mackenzie Delta would not have had sufficient energy reserves in 1973 to lay an average clutch of eggs (Table 5). Only females that were approximately 159 gm heavier than average at the onset of laying at the Delta (Table 7) would have been able, theoretically, to lay an average sized clutch. Female mallards displaced from the latitude of Tofield in 1973 would probably not have had sufficient energy reserves to nest in

the Delta. Data in Table 7 suggest that female mallards of average weight, homing directly to the Delta in 1974, could have laid only about half the average clutch for that year. Because 1974 average clutch size was only 7.2 eggs/clutch (Table 5), average and below-average weight female mallards probably would not have nested at all.

These calculations (Table 7) for pintails indicate that female pintails, which homed to the Mackenzie Delta in 1973, would probably have had sufficient fat stores to lay an average clutch (8.5 eggs; Table 5), whereas displaced females probably would not have laid at all. Female pintails of average weight, that homed to the Delta in 1974, would have had a clutch size slightly lower than the average.

Results based on calculations of energy requirements do not disagree with the actual reproductive potential data for pintails. However, there is some disagreement with the actual data for mallards: the calculations of energy requirements indicate that average weight mallards would probably not have been able to reproduce in either year, whereas actual data show that 75 percent were reproductive in 1973, and 67 percent in 1974.

The amount of stored energy, in body fat, a female has at the time of laying (which can be altered by proximate environmental factors) probably determines its reproductive potential in any given year.

DISCUSSION

This study was based on the premise that as conditions in the prairie-parkland region deteriorated for nesting waterfowl (as available surface water disappeared following drought conditions), increasing proportions of the population, that were unable to find acceptable habitat, moved farther and farther north. Further, this northward movement reduced the reproductive output of those involved. The former hypothesis is present in the literature (Crissey 1961; Hansen and McKnight 1964); the latter was the subject of this investigation.

Regarding the former hypothesis, I believe it is appropriate to critically analyze the data presented, and to determine the extent to which the hypothesis stands up in view of additional data since Crissey (1961) and Hansen and McKnight (1964) proposed it.

Numbers Collected

I was less successful in collecting samples of mallards and pintails in the Mackenzie Delta than at Tofield for two reasons: 1) the frequency with which ducks, particularly mallards, were encountered in the Delta was lower than at Tofield, and 2) the restriction of travel to water courses in the Delta made waterfowl less approachable there than at Tofield.

The scarcity of mallards in the Mackenzie Delta reflected lower population levels in the area sampled, in recent years. This decline has been documented through the U.S. Fish and Wildlife Service. The mean number of mallards and pintails counted in the Delta from 1955 to 1964

was significantly greater for both species ($P < 0.05$ and 0.01, respectively) than the mean number counted between 1965 and 1974 (Table 8). These differences reflect a general decline in the number of both species in the Mackenzie Delta over this 20-year period. Furthermore, in 1974, the numbers of both mallards and pintails counted in the Delta were near the lowest recorded (Table 8).

Crissey (1961) proposed that the number of waterfowl recorded in aerial censuses of the arctic breeding grounds was inversely correlated with the number of May ponds on the prairies. Hansen and McKnight (1964:119) attempted to determine if this correlation existed and indeed they concluded that as "prairie potholes disappear and their associated waterfowl population diminishes, the duck population expands in the north." However, upon testing the data presented by the above authors, no significant inverse relationship was found between numbers of ducks in the north and numbers of May ponds on the prairies (Fig. 8). Therefore, their premise is not supported by the data. Furthermore, I found that the relationship between the numbers of mallards and pintails in the Mackenzie Delta and the number of May ponds on the prairies (Table 8) from 1955 to 1974 was not statistically significant (Fig. 9).

It is noteworthy that, in dry years, the assumed loss of ducks from the prairies and parklands was never completely accounted for by increases in measured numbers in the north (Hansen and McKnight 1964). In fact, the proportion of missing birds accounted for was low, rarely exceeding 40 percent. Hansen and McKnight suggested that missing ducks were located between areas censused.

The data presented by Hansen and McKnight (1964) provided evidence

Table 8. May prairie-parkland pothole counts and corresponding Mackenzie Delta duck indices.

	Year	Duck Index[1] Mackenzie Delta ('000)		Adjusted[2] May ponds ('000)
		Mallards	Pintails	
	1955	11.7	15.8	7303
	1956	8.1	17.0	4857
	1957	6.0	22.6	3325
	1958	13.9	84.5	3241
	1959	22.6	84.6	1955
	1960	18.1	116.4	3647
	1961	24.6	43.5	1654
	1962	17.0	41.7	2275
	1963	12.3	16.2	2475
	1964	2.2	13.2	2743
	1965	8.0	34.0	3536
	1966	10.0	7.8	3724
	1967	6.6	4.9	3782
	1968	5.8	5.3	1636
	1969	14.5	10.0	2963
	1970	8.6	6.6	4389
	1971	5.8	6.7	3865
	1972	6.6	9.1	3435
	1973	5.1	13.3	1888
	1974	2.2	7.9	5589
Averages	1955-1964	13.6	45.5	3442
	1965-1974	7.3	10.6	3562

[1]Data courtesy of A. Martell (Boreal Institute for Northern Studies) and J. Voelzer (U.S. Fish and Wildlife Service).

[2]Data courtesy of D. Anderson (U.S. Fish and Wildlife Service).

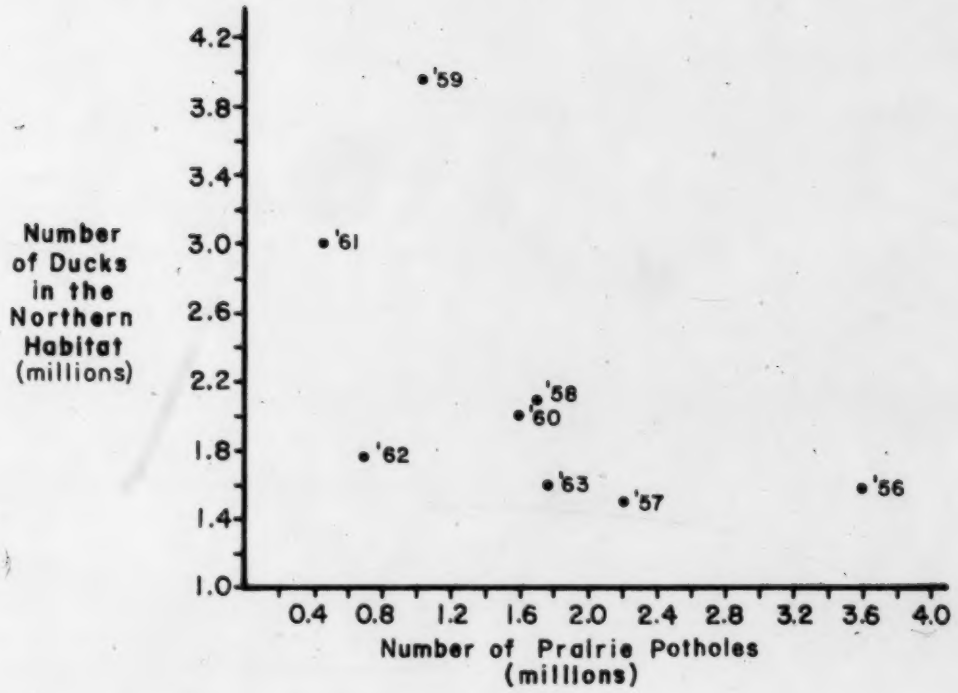

FIGURE 8. Relationship between the number of ducks in the northern habitat and number of prairie potholes (1956-63). Data from Hansen and McKnight (1964).

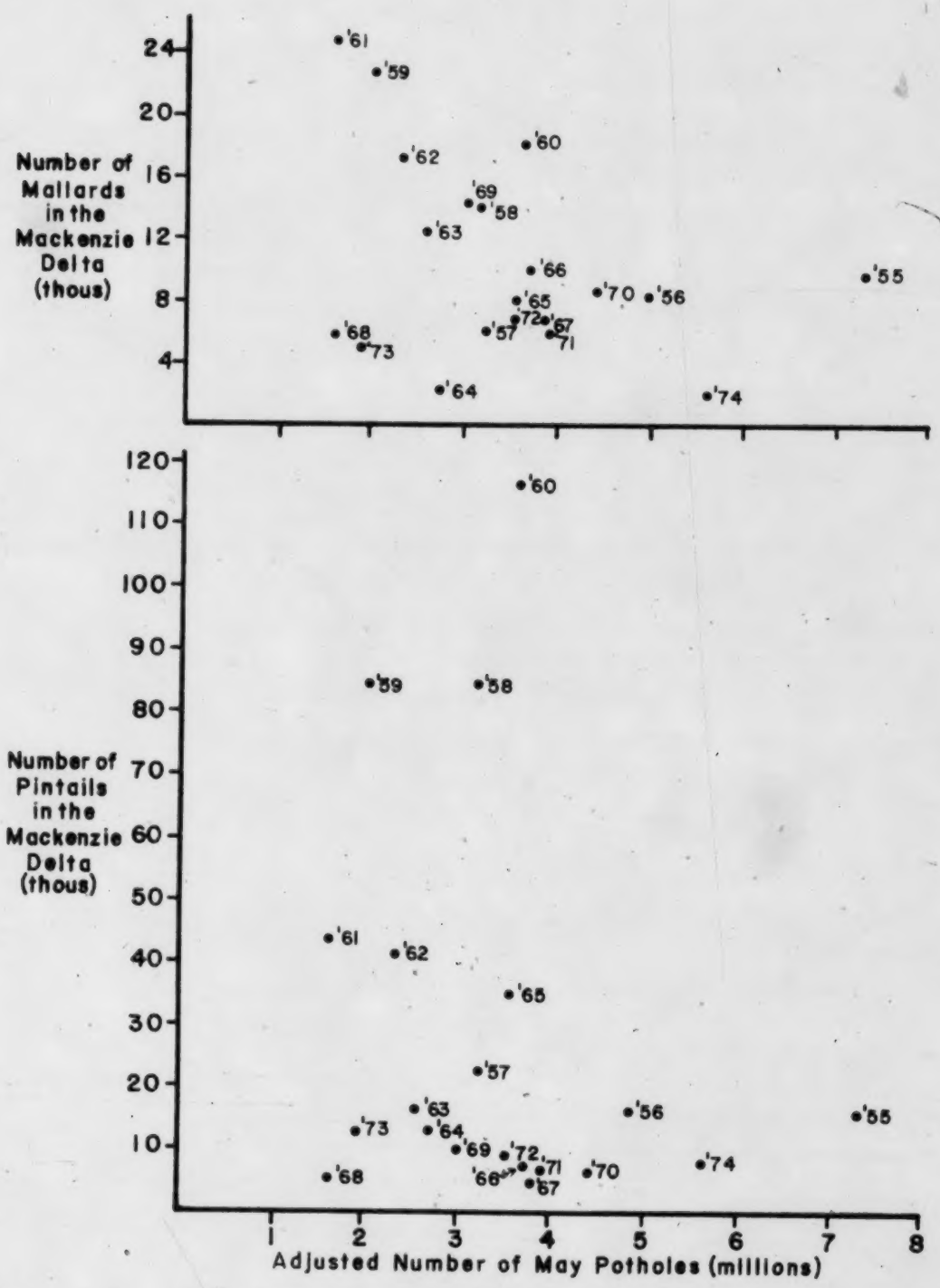

FIGURE 9. Relationship between number of mallards and pintails in the Mackenzie Delta and the number of May potholes on the prairies, adjusted for visibility. Data on numbers of ducks supplied by A. Martell (Boreal Institute for Northern Studies) and J. Voelzer (U.S. Fish and Wildlife Service) and potholes by D. Anderson (U.S. Fish and Wildlife Service).

that as drought conditions intensified the density of dabbling ducks, per pothole on the prairies, initially increased. However, as continental populations declined, presumably due to decreased reproduction, fewer ducks returned to the prairies; thus, density dropped off even though numbers of prairie potholes may continue to decline (Table 8). This implies that prairie dabbling ducks are able to condense to some extent their breeding territories (or become more tolerant of their neighbors) and thus reduce the numbers of ducks which might be displaced northward.

In support of their hypothesis, Hansen and McKnight (1964) provided a few data on the relationship between prairie-banded ducks recovered in Alaska and drought years on the prairies. They mention three species. Two of these (wigeon [*Anas americanus*] and pintail) did not support their hypothesis because as many birds were recovered following wet as following dry years, but the third (mallard) did support their hypothesis. However, only seven prairie-banded mallards were recorded, and because the authors gave no data on sex or age when these birds were recovered, it was impossible to judge to what extent they were prairie-banded males mated to homing arctic-reared females and whether the recoveries were direct or indirect. These authors also provided sight records on species which they claimed were more abundant in Alaska in drought years on the prairies. These are of questionable value as they cover only an 8-year period, split between two locations (Ft. Yukon and Tetlin, Alaska). The Ft. Yukon data included the years 1953-1956 (wet years on the prairies), which preceded the years of drought (i.e., 1958-1962). Therefore, data from Ft. Yukon miss key years for comparison. The Tetlin data, which began in 1957, excluded data for years of wet prairie conditions, and therefore allow for no

comparison of numbers of ducks observed in the arctic in wet years.

More recent investigators also have reported significant inverse relationships between the number of pintails in the north (boreal forest and arctic) and the number of potholes on the prairies (Smith 1970), and between band recoveries in Siberia of pintails banded in interior North America and years of drought on the prairies (Henny 1973). Smith (1970), using data from 1959 to 1968, was able to correct for two obvious deficiencies in the 1964 paper by Hansen and McKnight: 1) he used statistical methods in data analysis, and 2) he was able to correct for annual variations in size of the continental population of pintails to show a significant inverse relationship. Henny (1973) attempted to correct for a third deficiency in Hansen and McKnight's paper, that being the reliability of any conclusions based on raw aerial census data, in view of the great number of variables associated with these data (Martinson and Kaczynski 1967). Henny (1973) utilized aerial census data adjusted for visibility, using the most recently calculated adjustment factors (Pospahala *et al.* in prep. in Henny 1973).

As indicated above, the data presented by Hansen and McKnight show no significant correlation between numbers of arctic waterfowl and numbers of May prairie ponds. However, when their data are corrected for varying continental population size (by using the proportion of the continental population that is in the north), there is a highly significant inverse relationship ($P < 0.005$) between the proportion of the continental population of dabbling ducks in the north and numbers of ponds on the prairies (Fig. 10). When aerial census data are adjusted for visibility, this relationship becomes even more significant ($P < 0.001$).

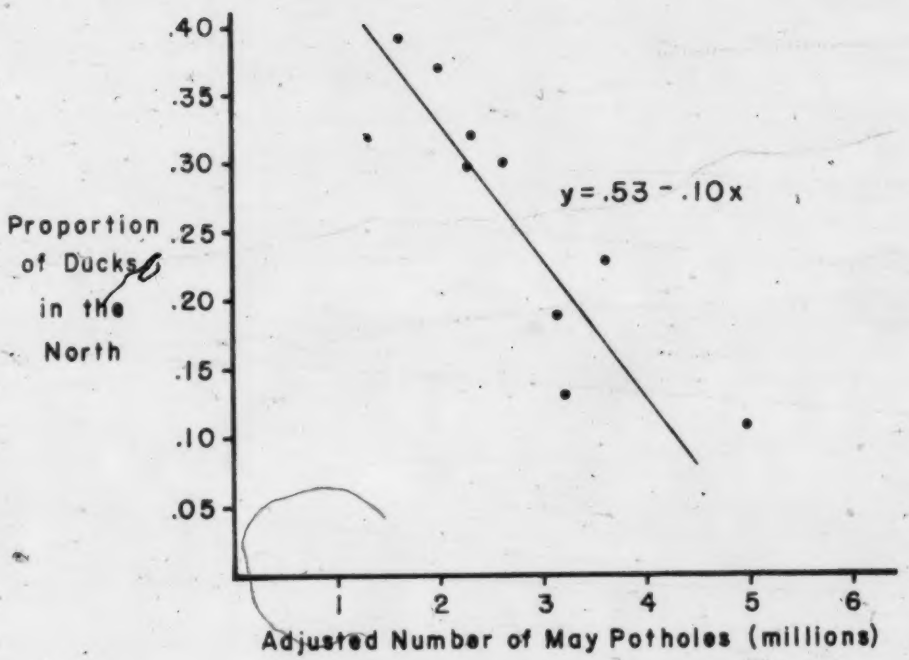

FIGURE 10. Significant inverse relationship between the proportion of the continental population of dabbling ducks in the north and the number of May prairie potholes, adjusted for visibility (1956-63). Data from Hansen and McKnight (1964) and D. Anderson (U.S. Fish and Wildlife Service) were used in constructing this figure. Continental population estimates from Hansen and McKnight (1964) are given in Appendix 3.

Thus the hypothesis should be restated in the following manner: as prairie potholes decrease in number, the proportion of the continental population of dabbling ducks in the north increases, and through reduced reproduction, continental populations decline.

The continental population of dabbling ducks varies directly with natality (and mortality) in the previous year. The proportion of this population that remains on the prairies is directly related to the number of May ponds on the prairies. The numbers of ducks lost on the prairies and not accounted for in the north (referred to as missing by Hansen and McKnight 1964) are probably nonexistent and merely reflect decreasing trends in the size of the continental population of dabbling ducks during periods of drought.

Fortunately, during one year of this study (1973), drought occurred on the prairies with an apparently associated displacement of mallards and pintails. This increase in proportion of continental dabbling ducks in the north in 1973 is shown by the aerial census data (Table 8).

In addition to smaller populations present, the weather conditions in the Delta in 1974 were such that I was unable to travel on more days than I could travel. Thus, the poor weather conditions also could have been responsible for the decreased 1974 Mackenzie Delta sample sizes. Although I lengthened the collection period to increase sample size in 1974, this attempt was nullified, due to these weather conditions, and I actually collected fewer ducks than in 1973. Therefore, lower population densities added to poor weather conditions were responsible for the lower sample sizes in the Delta than at Tofield.

Reproductive Status

The proportion of ducks collected in the pre-ovulatory state at Tofield was greater than that among Mackenzie Delta ducks. This probably was due to the time at which I concentrated my collections. At Tofield, I shot ducks at a somewhat earlier stage in the reproductive cycle, mainly because ducks were more readily available. In the Delta the ease of mobility was so reduced before break-up, that most birds were shot afterwards. Since most ducks began laying about the time of break-up, relatively few pre-laying females were collected.

The lack of significant differences in numbers of pre-ovulatory and ovulatory females collected, between years, and between species, within a given area, indicated that these collection periods corresponded to similar times in the laying schedule of both species. The large proportion of ovulatory females in the samples indicated that the period of collection corresponded with the period when most were laying.

Low numbers of ducks in the post-ovulatory category probably reflected their low availability in the population sampled. This was because females in this category spend most of their time incubating.

The high numbers of ovulatory females and low numbers of pre-ovulatory and post-ovulatory females in the samples suggest that collection periods were optimal (yielded the most useful data) for the purposes of this study.

Based on the low numbers of birds in the pre- and post-ovulatory category (Table 2), there was a low incidence of renesting among both species collected at Tofield, especially in 1974; no renesting was

recorded among ducks collected in the Mackenzie Delta. The latter observation agrees with the findings of Marshall (1952) and of the speculations of Smith *et al.* (1964) and Ricklefs (1973). Barry (1967: 174) reported that arctic nesting geese must initiate laying within 10 days of arrival on the breeding grounds or "reproductive attempts for that season are stopped." He believed that after this period there was insufficient time and energy for successful reproduction. As northern bred pintail ducklings require only between 5 and 6 weeks to fledge (Gollop pers. comm. in Maher and Nettleship 1968), only 10 to 11 weeks are required for successful reproduction of pintails in the north (for mallards this time period is unknown, but is presumed similar). Thus, if ducks do not leave the Mackenzie Delta until approximately mid-September (Porsild 1935), pintails have sufficient time not only to reproduce, but also to renest. Therefore, I believe that lack of energy is the more important factor in pintails as previously mentioned. With the inability to renest, the reproductive potential of this population is automatically reduced.

The higher incidence of renesting in females collected at Tofield in 1973, compared to 1974, may have been due to the lateness of the collection period in 1973 and/or indirectly to the drought conditions in 1973. For reasons that are discussed in the next section, I believe that nesting was delayed in 1973 and that collections therefore took place at approximately the same phenological period, in the 2 years. Regarding the latter possibility, I can only speculate that rapidly declining water levels in 1973 may have allowed mammalian predators to cross water barriers, thus increasing nest predation on islands. Also, the dry conditions of 1973 allowed land owners to burn stubble fields and slough

edges earlier and more effectively (Fritzell 1975) thus destroying more nests than in 1974.

Renesting allows a female to compensate for loss of the initial clutch (Cartwright 1952; Sowls 1955; Keith 1961). Although the clutch size in renesting attempts is generally smaller than in initial attempts (Sowls 1955; Coulter and Miller 1968), the ability to renest increased the reproductive potential of Tofield ducks, over those in the Mackenzie Delta.

It is evident, from Table 2, that most females collected at Tofield, and classed as being not reproductively active (9.4 percent of the total sample in 1973 and 1.6 percent in 1974), fell into the non-ovulatory category. In the samples from the Mackenzie Delta, of the non-reproductive individuals (39.3 percent of the total sample in 1973 and 31.6 percent in 1974), most were in the non-ovulatory category in 1973, but in the atretic category in 1974. I believe that the low number of females showing atresia at Tofield was due to their ability to renest. When initial clutches were lost, ducks at Tofield probably had the time and available energy to produce a second or even third clutch, and thus most did not resorb follicles.

The Delta environment, in 1973, may have failed to provide the correct stimuli for follicular development to those displaced ducks (especially pintails) which were inexperienced in an arctic situation. However, insufficient available energy was the more likely cause of ovarian inhibition. In 1974, atresia was common in the Delta, probably because of the late spring and related delayed laying; energy stored for developing ova was probably required in daily maintenance, resulting in resorption of deposited yolk.

The proportion of non-reproductive females in the populations sampled may have been greater than these data suggest (Table 3). This is because females that have lost the desire to breed sometimes leave the breeding areas and go with males to molting grounds (Porsild 1935; Coulter and Miller 1968), usually large marshes (Sowls 1955), and therefore would be unavailable for collection, especially on the Tofield study area. As some female mallards and pintails had completed their clutches when collected, and males abandon their mates when incubation begins (Hochbaum 1944; Sowls 1955; Lebret 1961), I assume that at least some males were leaving the study area during the collection periods and that they were accompanied by some non-reproductive females.

I was unable to determine the age of ducks collected (Appendix 1). Thus I do not know the age of the birds falling into the various reproductive categories. The literature suggests that yearling females are most vulnerable to displacement (McKinney 1965). It is also unknown what proportion of the Mackenzie Delta samples in 1973 consisted of drought-displaced ducks. Much more research must be done to determine what portion of the eleven non-reproductive females in the northern samples in 1973 were in fact yearling birds, which homed to the prairies or parklands and were displaced to the Mackenzie Delta.

The different proportions of reproductively active female mallards and pintails between Tofield and the Mackenzie Delta (Table 3) have direct implications on the reproductive potential of ducks in these locations. The reduced proportions of mallards and pintails that were reproductively active in the Mackenzie Delta samples are evidence that these populations of ducks have a lower potential for the production of young than those at Tofield.

Clutch Initiation

At Tofield, which is 15 degrees of latitude south of Inuvik, spring thaw occurs approximately 1 month earlier than in the Mackenzie Delta. This accounts for the difference in date of onset of laying found between these two locations.

The onset of laying in ducks has been related to ambient temperature and precipitation (Sowls 1955; Yocum and Hansen 1960; Keith 1961; Dane 1966; Smith 1968; Pospahala *et al.* 1974). I examined these two climatic factors in relation to differences in date of initiation of laying between years at Tofield, where laying began on April 17, 1974, 14 days earlier than in 1973.

Investigation of the weather records, 1 week prior to the first recorded date of laying at Tofield to the end of April (April 11-30) (Appendix 2), revealed that the mean maximum temperature was higher, and the mean minimum temperature was significantly higher ($P < 0.05$) in April 1974, than in 1973. Also, total precipitation (rain and snow) was 55 percent less during this period in 1974. Thus the difference in onset of laying in the 2 years seems best explained by the climatic conditions of the 2 years; 1973 was colder and wetter. The difference between the collection periods at Tofield in the 2 years was thought not to have been a significant factor in the different calculated laying periods, due to the paucity of overlap in dates of clutch initiation between years especially in mallards (Fig. 2).

It is noteworthy that during the week before most nests were initiated (Fig. 2), the mean maximum temperature exceeded 10° C in Tofield in both years, and in the Mackenzie Delta, in 1973. In 1974, in

the Mackenzie Delta, the mean maximum temperature for 1 week did not exceed 10° C until the second week of June.

In the Delta, besides temperature and precipitation, break-up and associated flooding influences the onset of laying. Mallards and pintails usually begin to arrive in the Delta in the second week of May (Porsild 1935; local Inuit pers. comm.). By this time much of the land surface in the Delta is free of snow, but ice still remains on the water courses, except near the edges, where rising water levels in the distributaries create open leads. Thus, although nesting habitat apparently is available when the ducks arrive, they do not seem to nest immediately, probably because they are not physiologically ready (Irving 1960). In the last 10 days of May 1974, pairs were observed spacing themselves over the breeding area.

The onset of laying by mallards and pintails in the Mackenzie Delta (Fig. 2) may be correlated with time of break-up of ice cover on the river. Break-up of the river occurred on May 30 and 31 in 1973, and June 8-11 in 1974 and appeared to be related to minimum temperatures (Appendix 2). However, as Mackay (1963) and MacKay and Mackay (1972) pointed out, break-up of the Mackenzie Delta occurs in response to upstream input of melt-water, flushing the downstream ice into the Beaufort Sea. The majority of reproductively active birds, sampled in the 2 years, nested on, or after, break-up.

Mallards and pintails showed the same reproductive cycle in each study area, except for the northern sample of mallards in 1974, which nested earlier than pintails. This may have been due to small sample size. However, in the light of the forthcoming discussion on the energy requirements for reproduction in the Mackenzie Delta, it is apparent that female mallards may have had to lay early or not at all.

Delaying the onset of laying until after break-up would appear to have selective advantage, because early nests would be subject to flooding. When environmental factors delay the initiation of laying, reproductive status may change rather abruptly from pre-ovulatory to atretic. Thus, reproductive potential may be reduced through decreased proportions of the population that are reproductively active, or through reduced potential clutch size.

Potential Clutch Size

The most common problem in this part of the study was that of deciding which follicle(s) would have been the last to develop. Once this had been established, the potential clutch size could be estimated, giving another measurable parameter of reproductive potential. The use of a gap in the frequency distribution of pre-ovulatory follicles (in millimeter size classes) is thought to be fairly accurate for the ovaries of females nearing completion of their clutches. The reliability of this gap as a cut-off point in ovaries of females in earlier stages of laying is unknown. However, a gap did consistently appear at the onset of laying or shortly thereafter, allowing consistency in the analysis of these females. Clutch size estimations based on this technique were not significantly different from those based only on post-ovulatory follicles of ducks which had completed their clutches.

As a follicle develops, the deposition of white yolk precedes that of yellow yolk (Romanoff and Romanoff 1949). Thus younger follicles appear white and older follicles appear yellow. The degree of reliability of using the smallest yellow follicle as the criterion for the cutoff point is, again, unknown. However, in the estimation of potential clutch size, for the 19 mallards and pintails for which this

criterion was used, an average potential clutch size of 9.4 eggs/female was estimated, which was not significantly different from the average potential clutch size based on other criteria. Had I included just one more size class in this determination, average potential clutch size jumped to 12.6, which is significantly higher ($P < 0.001$) than the average clutch size based on other criteria. If one less size category had been used, the average potential clutch size of these 19 females would have been 7.7 eggs/female, which is significantly lower ($P < 0.001$) than all other estimations of potential clutch size. Although I attribute a rather low level of confidence to this method of potential clutch size determination, it has proven to be a consistent criterion, which was statistically acceptable. This technique was used only if the largest pre-ovulatory follicle was at least 12 mm in diameter along the stigma.

The average potential clutch sizes obtained in this study (Table 5) for Tofield mallards and pintails were somewhat higher than actual average clutch sizes obtained in the Alberta (Smith 1971) and Saskatchewan (Stoudt 1971) parklands. However, the actual values contained a far greater proportion of renests, which are of smaller size (Sowls 1955). The Mackenzie Delta average potential clutch sizes were usually lower than the actual parkland values. The smaller average potential clutch size of females collected in the Mackenzie Delta is further evidence that these ducks have a lower reproductive potential than those collected at Tofield.

Why were the potential clutch sizes of mallards and pintails reduced in the north? Some of the first papers discussing waterfowl

clutch size were by Lack (1967; 1968a; 1968b). He hypothesized that the average clutch size of waterfowl (taking into consideration egg size differences between species) has ultimately evolved in relation to the average availability of food for the female at the time and place of laying. Klomp (1970) and Immelmann (1973) have agreed with Lack's hypothesis. However, Johnsgard (1973) has expanded on Lack's hypothesis and suggested four ultimate factors in the evolution of clutch size in waterfowl. Johnsgard mentioned first Ryder (1970), who suggested that female Ross' geese (*Anser rossii*) require maximal amounts of pre-breeding fat reserves to provide them with enough energy to complete incubation, and to provide the egg with sufficient energy to allow the young to survive until they can feed. Therefore, it is not the availability of food to the female at the time of laying but the amount of reserve energy in the form of stored body fat that is selected for. The storage of large fat reserves is an adaptation of arctic-nesting geese, which allows them to lay a normal-sized clutch regardless of the amounts of available food on the breeding grounds at the time of laying (MacInnes *et al.* 1974).

Arctic-nesting mallards and pintails probably cannot be as dependent upon fat reserves as are arctic-nesting geese, because they lay a greater number of eggs, which constitute a greater proportion of their body weight. Therefore, it is probably necessary that they have at least some proteinaceous food available during laying or clutch size probably would be reduced. In these ducks a combination of both fat reserves and available food on the northern breeding grounds probably represent the ultimate factors in the evolution of clutch size. Thus, when proximate factors determining clutch size, such as temperature,

precipitation, spring break-up and its associated flooding, combine to delay nesting and put greater energy requirements for body maintenance on these ducks prior to nesting, the potential clutch size should be reduced so that females can maintain a high level of parental effectiveness through incubation. That is, the greater the energy reserves remaining after a female has completed its clutch, the less time is spent feeding and the more time incubating. This increases the probability of success of the clutch and survival of the adult. The late date at which most of the 1974, Mackenzie Delta pintails nested, may have been too long after arrival for the development of normal numbers of ova from the remaining amount of stored fat. The fact that all reproductively active Mackenzie Delta mallards collected in 1974 nested early implies that mallards in the north may utilize their fat reserves more quickly or that they are unable to store relatively as much fat as pintails. Had these females not nested early they probably would not have nested at all (as was the case with all other mallards collected in the north in 1974). Further, clutch size was reduced in those that did nest.

Johnsgard secondly proposed that egg predation, during the laying period, may limit clutch size. The probability of pre-incubation predation increases with increasing clutch size, because for each additional egg laid the nest takes longer to complete, thereby exposing the nest to predators for a longer period. This hypothesis is based on the assumption that most clutch predation occurs during the laying of the clutch. To demonstrate this Johnsgard cites the example of Choate (1967) who found that in American eiders (*Somateria mollissima*), 66 percent of all nest predation, in one year, occurred on incomplete clutches.

However, there is mounting evidence that the probability of nest predation increases after nests have been located by humans (Dwernychuk and Boag 1972). Therefore, until this problem is resolved the importance of predation as an ultimate factor in the evolution of clutch size is questionable.

Johnsgard's third ultimate factor in the evolution of clutch size involves decreasing parental effectiveness with larger clutches. Mendall (1958) found reduced hatching success among ring-necked ducks (*Aythya collaris*) with larger clutches. The effect is obvious in tree-hole-nesting ducks that lay so many eggs that they are layered, but ground-nesting birds should be able to turn over and warm the eggs so that all are kept sufficiently warm. Also Eygenraam (1957) and Gollop (1965 *in* Dzubin and Gollop 1972) reported that larger than normal broods of mallards may have higher than normal mortality rates. Cooch (1961) found this true in lesser snow geese (*Chen hyperborea*). Johnsgard offers no explanation as to how mortality of the young occurs. I believe that mortality is caused mainly by cold, wet weather and/or predation, which are proximate factors in clutch size. Therefore, I do not consider decreased parental effectiveness an ultimate factor in the evolution of clutch size.

The fourth idea relates to species with a restricted optimal breeding period or need to synchronize hatching into an optimal hatching period, as in the arctic. Bengtson (1972) found that, in Iceland, survival of late-hatching broods of ducks was not as great as those which hatched earlier in the season. Cooch (1961) found this to be true also for lesser snow geese. In the case of geese there seems to be just enough time during the summer for successful reproduction. Therefore,

they arrive on the breeding grounds physiologically ready to nest. Any delay reduces their reproductive potential. I believe the ultimate factor here is that which was discussed as Johnsgard's first suggestion. As ducks have more than enough time to successfully reproduce in the Mackenzie Delta, optimal breeding periods or synchronized hatching periods may be important. However, I believe these to be controlled by proximate factors, which would not ultimately affect clutch size as would the energy available for the female at the time of laying.

I believe, therefore, that the first hypothesis of Johnsgard, which was based on the work of Ryder (1970) represents the most likely ultimate factor in the evolution of clutch size of mallards and pintails nesting in the Mackenzie Delta.

Implications of the Calculated Energy Requirements for Reproduction in the Delta

The hypothetical calculations of energy requirements for reproduction in the Mackenzie Delta were based on many assumptions and approximations. However, the results have some interesting implications. The fact that all hypothetical average weights at laying, for mallards, were much below the average weight at laying of those females that did lay (Table 7), suggests that female mallards must store very large amounts of fat in the south in order to lay an average-sized clutch in the Mackenzie Delta. The actual data indicate that a large proportion of the Mackenzie Delta mallard samples were reproductively active (Table 3). Therefore, either the hypothetical calculations are in error, or, as discussed below, the samples were biased because non-reproductive mallards were, perhaps, not present on the study area. Even if large fat stores are deposited, any delay in laying, as in 1974, could quickly deplete

reserves and reduce reproductive potential (assuming an inability to ingest sufficient energy per day to maintain body weight). Reproductively active mallards collected in 1974, nested early and may not have been able to lay at a later date, because a delay would have caused reduction of energy reserves to the point where no eggs could have been produced. The average clutch size was, in fact, low (Table 5).

In mallards, maximal fat reserves would always be a prerequisite for laying a clutch. The combined effect of increased energy expenditure and shorter breeding season, the further north they go, may explain why the latitude of the Mackenzie Delta is the northern limit of their breeding range in northwestern Canada (Godfrey 1966). Krebs (1971) demonstrated with the great tit (*Parus major*) that as the limit of the breeding range is approached and more marginal habitat is found, the reproductive success of the population dwindles. Thus the Mackenzie Delta mallard population probably only just maintains itself or may even depend upon periodic immigration of birds from the south, some of which may reproduce in years when conditions in the south may force them to move northward.

Pintails homing to the Mackenzie Delta seem better able to cope with arctic nesting than mallards. Female pintails arrived in the Delta in 1973 with what, hypothetically, appears to be just the right amount of reserve energy to nest and lay average-sized clutches. However, in 1974 although they arrived in good condition, nesting was delayed in most, and probably due to excessive expenditure of energy between arrival and laying (Table 7), average potential clutch size was reduced (Table 5).

Displaced females of average weight on arrival at Tofield used stored energy seeking breeding space on the prairies and in getting to the

Delta, and therefore, probably very few nested in the Mackenzie Delta (Table 7). However, those which had above average fat stores would probably have been able to lay a clutch of eggs. Because the actual clutch size for pintails in 1973 in the Delta was only slightly less than for 1973 Tofield pintails (Table 5), I suggest that most displaced females were non-reproductive, but that those that did nest laid near normal-sized clutches. This hypothesis was suggested also by Hansen and McKnight (1964).

The hypothetical calculations indicate that displaced females arrived at the Mackenzie Delta deficient in stored energy, suggesting that most would be non-reproductive. In effect, the northward movement of displaced mallards and pintails might be considered a molt migration. Such northward migrations are known in immature and non-breeding Canada geese (*Branta canadensis maxima*) (Sterling and Dzubin 1967), and Gollop (1965b *in* Anderson and Henny 1972) reported minor northward movements of adult mallards in the year of banding at Kindersley, Saskatchewan.

Sterling and Dzubin (1967:367) proposed that "the molt migration revolves about an increased survival of the popula-segments [*sic*] that move northward to molt." They suggest that reduced predation and unlimited food will reduce the number that would succumb to natural deaths than if these ducks remained on the breeding grounds. Also, competition for food would be reduced between breeders and non-breeders. In the Mackenzie Delta duck populations, large numbers of molting males and non-breeding females were counted by Porsild (1935). I observed that molting pintails and wigeons were found mostly along main channels, and I will assume, therefore, that the molting males and non-breeding

females, observed by Porsild, were present predominantly in such areas. Most nesting occurred along small creeks and lakes. Thus molting and brooding areas were probably separate. Porsild saw only "a few" molting mallards in 1934, as I did in 1973-74, suggesting that this species may go elsewhere to molt; however, it is not known where.

I believe that it is to the advantage of birds which are unsuccessful in establishing breeding territories on the southern breeding grounds to continue to search for breeding space, to the north, rather than simply to sit out the summer in a non-reproductive condition in the former locality. This behavior may have been selected for because birds with no reproductive potential in the prairie-parkland region may have some reproductive potential outside this region. By dispersing, they do not depress the reproductive potential of breeders, and they increase their own probability of nesting in that season. In those displaced females that do not nest, nothing is lost and they are able to molt, presumably in relative safety, so that in the next breeding season they can return to try again.

The hypothetical calculations indicate that the reproductive potential of mallards and pintails in the north is probably dependent on the availability of food, in combination with the amount of stored fat at the time of laying. This amount of stored fat is dependent on whether the duck is displaced or normally homes to the Mackenzie Delta, and on the environmental conditions, which determine the length of time between arrival and laying.

CONCLUDING DISCUSSION

The results of this study have shown that the reproductive potential of female mallards and pintails is significantly lower in the Mackenzie Delta than at Tofield. Lower reproductive potential resulted from a lower proportion of reproductively active individuals in the northern populations, lower average potential clutch size, and apparent lack of renesting in ducks taken in the north.

In 1973, drought conditions prevailed in the prairie-parkland region, whereas 1974 was very wet. In 1973, possibly as the result of drought-displacement, many more birds were present in the north, than in 1974. The Mackenzie Delta, and probably most of the arctic, experienced a cold late spring in 1974 compared to 1973. Possibly, large proportions of drought-displaced birds present in the samples shot in 1973, and the late, cold spring in 1974, produced the lower reproductive potential among female mallards and pintails collected in the Mackenzie Delta, than at Tofield during this study.

Low reproductive potential in the north in 1973 was due, mainly, to the lower proportion of reproductively active birds in the samples. This was attributed to displaced females arriving in the Delta with insufficient energy reserves to lay a clutch of eggs. Unfortunately, I was unable to determine the age of ducks collected. This prevented any investigation of the correlation between reproductive status and age of the birds. Thus, it is not known whether non-reproductive females were yearling birds, the age class most likely to be drought-displaced. In 1974, however, proportions of reproductively active ducks in the samples, and average potential clutch sizes, were significantly lower in the

Delta than at Tofield. This was attributed to cold, wet weather and late spring break-up, which may have increased energy expenditure to the point where insufficient reserves remained for egg development. Thus, if females laid at all, they usually had a very low clutch size.

The ability to renest after the loss of initial clutches greatly increases reproductive potential. One major factor governing the ability of ducks to renest is the length of the frost-free season. Longer seasons permit earlier nesting and thus more opportunities to renest if there is sufficient energy available to the female. Loss of initial clutches may be affected by many factors, including date of onset of laying in relation to agricultural activities, as may bave been the case at Tofield during this study. Because renesting occurs in the north rarely, if ever, the reproductive potential of mallards and pintails nesting in the arctic may never equal the reproductive potential of these species in the prairie-parkland region.

The results of this study are not at variance with the hypothesis of drought-displacement. In fact, this hypothesis is the best explanation for the 1973 data. A reevaluation of the data presented by Hansen and McKnight (1964) did not support their hypothesis. However, when corrected for declining continental populations, the data did show a significant inverse relationship between the numbers of prairie ponds and the proportion of the continental population counted in the north.

Long-term studies involving massive banding programs and possibly radio-telemetry need to be undertaken to determine whether pairs of ducks, unsuccessful in establishing themselves on the drought area, are

then displaced to the north. Does this phenomenon involve a particular age class? How far do they go? What is their physical condition when they get there? These questions must be answered to fully appreciate the contribution made by the northern breeding grounds to continental waterfowl populations, when habitat conditions in the south deteriorate.

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APPENDIX 1. DETERMINATION OF AGE

The annual layering in hard structures such as scales, teeth and bone, has long been used for age determination in vertebrates. Different techniques based on the same principle have been used on all major classes of vertebrates. The most detailed review has been written by Klevezal and Kleinenberg (1969) on mammals. Only recently has anyone looked for annual layers in birds, the first being van Soest and van Utrecht (1971).

Although there have been attempts, it is interesting to note that, to my knowledge, there have been no publications involving this technique of age determination of birds in North America. There are two publications in the literature, which claim satisfactory results. One is the original description (van Soest and van Utrecht 1971) and another by Klevezal *et al.* (1972) from Russia.

Van Soest and van Utrecht (1971) decalcified bones in 5 percent HNO_3 for 10-15 hours and trimmed them to use the areas of bone where tendons were inserted. They found the tibiotarsus the best bone to work with in the mallard.

The ages of 8 mallards and 20 pintails were investigated in this study. Twenty-four were collected from the Mackenzie Delta and four from Tofield, of which two were known juveniles and two were known adults (one of each species in each case). These known-aged females were collected in the autumn and aged by plumage characteristics, according to Carney (1964).

I decalcified bones in RDO (DuPage Kinetic Laboratories Ltd.) for 14 hours. Over 2400 sections were viewed at 100X to 400X magnification. Sections were stained with Hiedenhain's hematoxylin or Harris hematoxylin except for the four known-aged specimens. This staining involved the use of an unpublished stain commonly used by the Histology Section of the Department of Zoology, University of Alberta. Tibiotarsi were sectioned just proximally to the epiphysis, the most appropriate site (van Soest and van Utrecht 1971). I also sectioned the total length of a tibiotarsus as well as both ends of the femur. The bones were sectioned at 10 microns. Much time was spent on the preparation, cutting and staining of each section. The techniques were overseen and occasionally performed by qualified histologists. However, I saw no section in which I was convinced that annuli were present. Possibly other bones could be tested or sections cut thicker (20 to 100 microns) (van Soest pers. comm). Nevertheless, as far as this study is concerned, I was unable to use this technique as a means of determining the age of ducks collected.

Van Soest and van Utrecht have summarized their work and that of their colleagues on the age determination of whales and beech martins (*Martes forma*). They found that in these species migration and food consumption (whales), but especially the sexual cycle has an influence on the growth of hard structures. Klevezal and Kleinenberg (1969) in a summary of work done on age determination in mammals from annual layers in the teeth and bones, found that growth of the wide band began in spring and ended in fall. The narrow band of the annual layer forms in the December to February period. North American researchers have followed basically the Russian techniques of age determination (Miller and Zwickel (1972).

The ideas dealing with age determination of mammals have been extended in an attempt to cover birds as well. However, much more work must be done to completely understand the significance of these annual layers and the best techniques to show them clearly.

APPENDIX 2. WEATHER RECORDS

The following weather records were taken from Vegreville, Alberta (46 km northeast of Tofield) and from Inuvik, N.W.T. (Anonymous 1973-74). Only the periods associated with onset of laying are included, from 1 week before the first recorded date of onset of laying (April 11 at Tofield and May 17 at Inuvik) to the end of April at Tofield, and to the latest recorded date of break-up in the Mackenzie Delta (June 11). Daily recorded maximum and minimum temperatures and precipitation in the form of rain and snow are presented. Snowfall has been converted to its equivalent in rain. Totals for precipitation and average temperatures are given for the data presented. Temperatures have been converted from Fahrenheit to Celsius degrees and precipitation from inches to centimeters.

Vegreville, Alberta

1973

Month	Date	Max (°C)	Min (°C)	Rain (cm)	Snow (cm)	Total Precip (cm)
April	11	17	-2	.08		.08
	12	13	3			
	13	2	-2		.79	.79
	14	0	-8			
	15	2	-15			
	16	7	-7			
	17	11	-4			
	18	10	-3	.38		.38
	19	11	0			
	20	7	2			
	21	10	-2	.08		.08
	22	13	-1			
	23	11	0	.10		.10
	24	9	-2			
	25	8	-5			
	26	14	-1			
	27	8	0	.84	.76	1.6
	28	1	-1	.56		.56
	29	6	-1	T		T
	30	9	-5			
Total				2.04	1.55	3.59
Mean		8.4	-2.7			

1974

Month	Date	Max (°C)	Min (°C)	Rain (cm)	Snow (cm)	Total Precip (cm)
April	11	6	-5	.09		.09
	12	3	0	.05		.05
	13	6	0			
	14	5	0			
	15	9	-2			
	16	7	-3	.03		.03
	17	9	-1			
	18	11	-2			
	19	9	-3	.05		.05
	20	4	-1	.08		.08
	21	11	-1			
	22	17	0			
	23	15	2			
	24	17	-2			
	25	25	2			
	26	16	6			
	27	11	0			
	28	16	-3	.05		.05
	29	19	2	.05		.05
	30	2	1	.05	1.02	1.07
Total				.59	1.02	1.61
		10.9	-0.5			

Inuvik, N.W.T.

1973

Month	Date	Max (°C)	Min (°C)	Rain (cm)	Snow (cm)	Total Precip (cm)
May	17	-3	-9		.05	.05
	18	2	-11			
	19	7	1	T		T
	20	11	2			
	21	3	-3	T		T
	22	2	-2	.03	T	.03
	23	5	-1			
	24	8	-1	.03		.03
	25	8	2	.58		.58
	26	22	2			
	27	17	1	.03		.03
	28	17	0			
	29	14	4	.08		.08
	30	11	3	T		T
	31	10	2	.71		.71
June	1	8	2	.13		.13
	2	8	1	T		T
	3	8	1	T		T
	4	15	2	.13		.13
	5	21	6	.51		.51
	6	21	11			
	7	17	4			
	8	12	3	T		T
	9	11	2			
	10	22	1			
	11	26	13			
Total				2.23	.05	2.28
Mean		11.6	1.4			

1974

Month	Date	Max (°C)	Min (°C)	Rain (cm)	Snow (cm)	Total Precip (cm)
May	17	15	-3			
	18	4	-3	T	T	T
	19	6	-6		T	T
	20	13	-1			
	21	13	-3			
	22	13	-1			
	23	1	-3		.15	.15
	24	2	-2		.08	.08
	25	-3	-2		T	T
	26	6	2			
	27	13	-6			
	28	11	-1			
	29	11	-5		T	T
	30	9	-7			
	31	8	1	T		T
June	1	6	-1			
	2	4	-1	.13	.23	.36
	3	4	-4		T	T
	4	1	-3		.11	.11
	5	9	-4		T	T
	6	18	3			
	7	17	1		T	T
	8	9	-2		.10	.10
	9	21	4			
	10	18	5			
	11	13	-2	T		T
Total				.13	.84	.97
		9.3	-1.5			

APPENDIX 3. CONTINENTAL POPULATION ESTIMATES (1956-63).

Year	Estimate of[1] total continental dabbling ducks (millions)	Total[1] prairie dabbling ducks (millions)	Total northern[1] dabbling ducks (millions)	Proportion of dabbling ducks in the North (millions)
1956	14.2	12.6	1.6	.11
1957	11.6	10.1	1.5	.13
1958	11.1	9.0	2.1	.19
1959	10.6	6.6	4.0	.37
1960	8.7	6.7	2.0	.23
1961	7.6	4.6	3.0	.39
1962	5.5	3.7	1.8	.32
1963	5.4	3.8	1.6	.30

[1]Data from Hansen and McKnight (1964).